

CHAPTER 4-9

ADAPTIVE STRATEGIES: SPORE DISPERSAL VECTORS

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CHAPTER 4-9

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Figure 1. Capsules of *Splachnum ampullaceum*, adapted for fly dispersal by both red colors and their odor. Note the special landing platform (**hypophysis**) below the cylindrical capsule. Photo by Michael Lüth, with permission.

Dispersal Types

Gao *et al.* (2000) examined the Chinese bryophyte flora and concluded that there are five classes of spore dispersal. These are wind dispersal, vapor-wind dispersal, water dispersal, decay dispersal, and insect dispersal. But more digging reveals that additional dispersal agents may be at work among the animals, including earthworms, spiders, molluscs, birds, and even mammals.

Hughes *et al.* (1994) concluded that the availability of specific dispersal vectors seems to have no influence on dispersal mode. I think that one could use flies that visit the **Splachnaceae** on dung to argue against that conclusion, but there do not appear to be any studies that attempt to correlate dispersal mode with availability of the vector.

For spores to gain access into the atmosphere, they must be expelled away from the capsule and join wind currents before they fall to the ground. One can flick a newly opened capsule and see clouds of spores emitted. It is likely that deer, rabbits, squirrels, and various small rodents bump these extended capsules, likewise sending up clouds of spores. To this end, the **peristome teeth** (Figure 2-Figure 4) of many mosses work like a saltshaker and permit only a portion of the spores to escape in one event. This helps to insure that dispersal takes place over an extended period of time and may then encounter more climatic conditions wherein some are suitable for good or even long-distance dispersal.

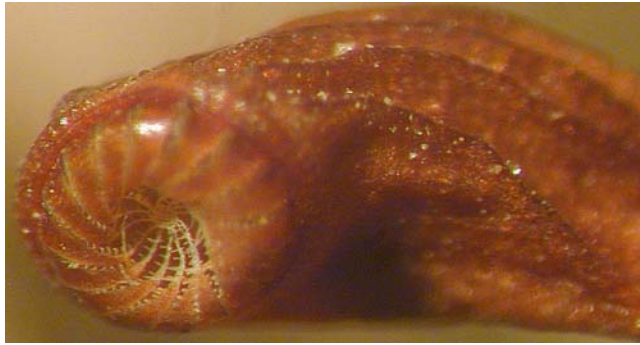


Figure 2. Peristome teeth of *Funaria hygrometrica*, showing the chambering that helps in the slow dispersal of spores. Photo by Michael Lüth, with permission.



Figure 3. Peristome teeth of *Aloina aloides* showing spaces between teeth that create a saltshaker effect to slow dispersal. Photo by Michael Lüth, with permission.

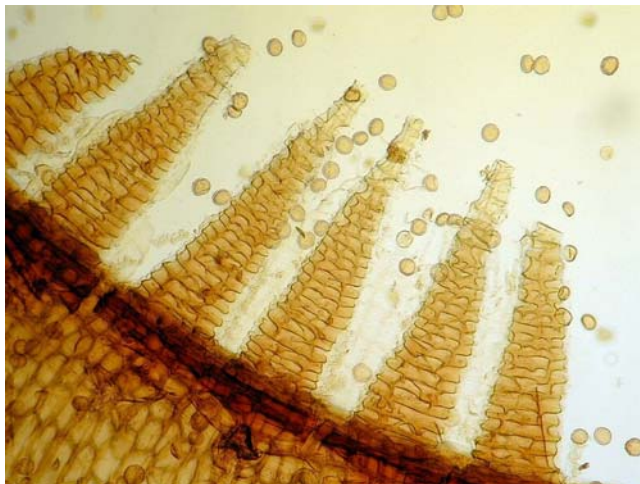


Figure 4. Peristome teeth and spores of *Ptychostomum pendulum*. Photos by Michael Lüth, with permission.

Wind Dispersal

Wind dispersal is assumed to be the rule among most bryophytes. But few data were available to support that concept for long-distance dispersal.

As we discussed in examining long distance dispersal, any propagule released from a greater height or elevation has a greater probability of being exposed to greater wind velocities (Greene & Johnson 1996). This means that greater heights increase the opportunities for wind dispersal. Campbell *et al.* (2001) contend that mosses have high immigration potential due to the wind-dispersal ability

of their spores. This would seem to argue against the conclusions of Hughes *et al.* (1994) that the availability of specific dispersal vectors has no influence on dispersal mode. As already discussed in the previous sub-chapter, successful wind dispersal relates to release height and falling time (slow for spores due to small size). Wing loadings in bryophytes are very low and probably have insignificant effect. Release height can be increased by explosive behavior of some capsules, and location on trees or at higher elevations likewise increases the opportunities to become airborne..

Lönnell (2011) reminds us that according to Stoke's law (Figure 5) spores can travel farther than larger diaspores of the same shape and density, given the same wind speed. [Stoke's Law: If particles are falling in a viscous fluid by their own weight due to gravity, then terminal velocity, also known as settling velocity, is reached when this frictional force combined with the buoyant force exactly balance the gravitational force.] Lönnell compared small seeds to large seeds, stating that, even if larger seeds can increase the buoyancy with features like pappi or wings, small seeds can still travel farther. Bryophyte spores lack such features as wings, but do possess pappi and other surface features. I am unaware of any study that has examined the role of variations in these markings as a means to facilitate wind dispersal. Perhaps they do, however, create buoyancy in water, permitting them to float and thus get dispersed farther.

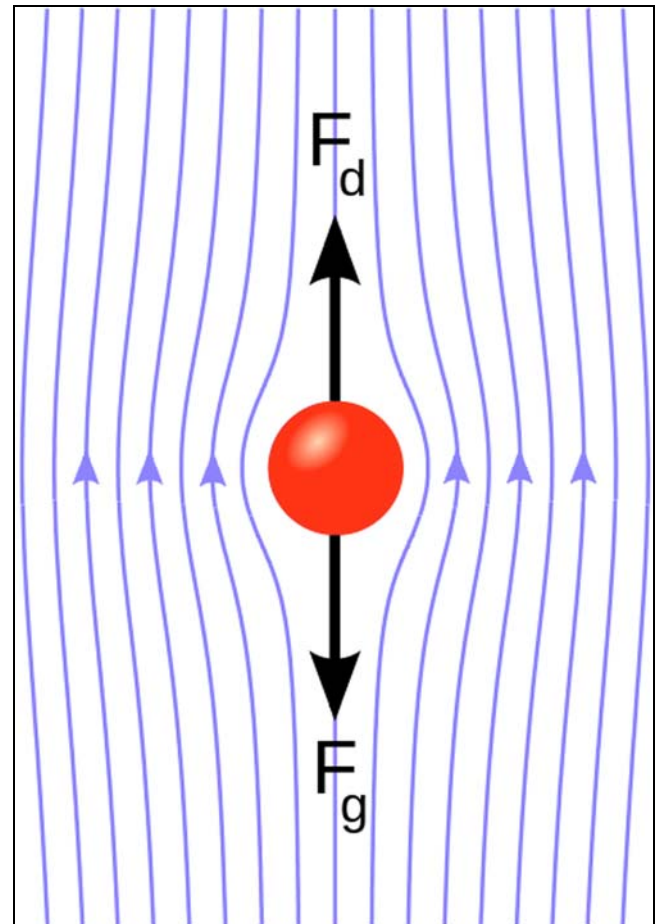


Figure 5. Stokes sphere showing movement of fluid around it. F_d is the frictional force, known as Stokes' drag. F_g is the force by gravity. Image from Wikimedia Commons.

We lack measures of density of bryophyte spores in the atmosphere, but experience with other organisms and particles are instructive. Schlichting (1978) tells us that there are 0.3-7.5 billion particles greater than 0.2 μm in diameter in one cubic meter of "clean air." And joining these organisms are spores of bryophytes. Puschkarew (1913) found an average of 2.5 protozoan cysts in a cubic meter of air, attesting to the success of somewhat larger structures being transported.

In sampling airborne algae in Michigan, USA, Schlichting (1964) found the greatest numbers of algae and protozoa between noon and midnight on cloudy days, with more during July and August than during September through May, although this may have related more to innate life cycles than to that year's weather conditions. The wind elevation angle (*i.e.*, horizontal vs vertical) seemed important in determining the number of organisms present; wind direction and speed seemed less important. Updrafts were more important than downdrafts or horizontal wind. Rainfall during the preceding 24 hours was detrimental to organism presence, most likely quickly washing them from the atmosphere. Sizes of the most common propagules ranged from the one-celled alga *Chlorella* with diameters of ca. 2-8 μm to those of cysts of the protozoan *Oikomonas*, for which living cells range up to 100 μm or more (without knowing the species, we cannot determine the size of the cysts, but they are likely to be similar). This range encompasses the majority of spore sizes of bryophytes.

But wind is constantly changing, and averages can be misleading. Sudden changes in direction can stir up tiny tornadoes that may dislodge and uplift spores. This might be especially true on glaciers. Bonde (1969) collected plant propagules from wind-blown debris on St. Mary's Glacier at 3350 m. He found 35 species of seed plants, but he also found viable parts of the moss *Polytrichum piliferum* (Figure 6), lichens, and *Selaginella*.



Figure 6. *Polytrichum piliferum*, a moss whose fragments are known from wind-blown debris. Photo by David T. Holyoak, with permission.

In the Southern Hemisphere, it appears that wind has played an important role in geographic distribution of bryophytes. Muñoz *et al.* (2004) found that there was a stronger correlation of floristic patterns with wind patterns than with geographic proximities, supporting wind dispersal for the arrival of many organisms in the Southern Hemisphere. These wind patterns followed "wind highways" that resulted in directional dispersal and distribution.

Felicitísimo *et al.* (2008) attempted to understand the role of global wind patterns in dispersal by not only wind data but also the pathway of a tracked seabird, the Cory's Shearwater (*Calonectris diomedea*). Birds are able to locate the pathways that require the least energy to carry them to their destination, going higher or lower, following mountains or other areas where updrafts and wind movement help to carry them where they need to go. The shearwaters followed the pathways predicted by the air pattern model, but when they reached the Atlantic sector of the Intertropical Convergence Zone, they were hindered by the near-surface westerlies. Only after these westerlies ceased were the birds able to cross this zone. Hence, we have evidence for seasonal differences in the most energy-effective pathways.

To understand the diaspore rain, it is necessary to trap the propagules, then culture them. Ross-Davis and Frego (2004) report success with diaspore traps using nutrient agar plates. These trapped diaspores grow well from both spores and vegetative propagules at indoor ambient conditions – so well that they need to be transplanted due to crowding. But patience is required; it takes nine months for them to reach a recognizable stage.

Splachnaceae

This family is best known for its spore dispersal by flies. But Walsh (1951; see also Bryhn 1897) has observed an alternative method – wind dispersal. He observed that in *Splachnum sphaericum*, when the capsule dried, the **peristome** teeth became reflexed, adhering to the outside of the capsule. From the inside, the spores were pushed out as the capsule dried and shrank. And the **columella** extruded from the capsule – a phenomenon known in only a few mosses. The spores form a ring around the top of the capsule and adhere to each other in clusters. The teeth remain hygroscopic and withdraw when moisture returns. Furthermore, the spores likewise withdraw and the capsule once more becomes turgid and swollen. This extension and intrusion of peristome and spores can continue to occur as moisture changes occur. When the peristome reflexes, it typically carries adhering spores away from the capsule.



Figure 7. Young capsules of *Splachnum rubrum* with **operculum** (cap) still intact on all but one capsule. Note that the umbrella-shaped structure is a **hypothesis** that occurs at the base of the capsule. Spores are housed inside the cylindrical structure above it. Photo by Michael Lüth, with permission.



Figure 8. Capsules of *Splachnum rubrum* that have shed their opercula. Note the exerted teeth and the ring of spores at the capsule opening. Photo by Michael Lüth, with permission.



Figure 9. Peristome of *Splachnum ampullaceum* with teeth reflexed against capsule and columella extruded at the center of the spore mass. Photo by Janice Glime.

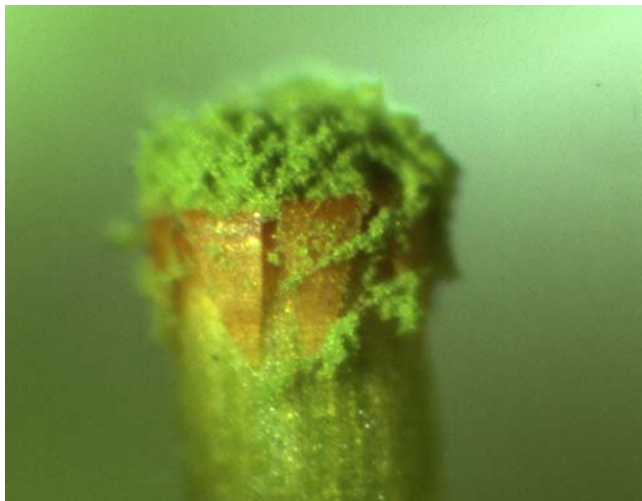


Figure 10. Peristome of *Splachnum ampullaceum* showing peristome teeth reflexed against the capsule and spore clusters clinging to them. Photo by Janice Glime.

When struck by a strong wind, the extruded clusters may extend from the capsules in either clumps or threads. Sometimes the wind causes the threads to bend back upon themselves, in which case the thread more closely resembles a clump. But in some cases the clusters or

threads may break loose, effecting dispersal. The stickiness of the spores is important in assuring that both genders arrive on the new substrate, hence making spore production possible in that generation. But Walsh was unable to observe the fate of these escaped spores. The dung substrate necessary for the life cycle to continue is rare relative to all the other possible landing substrates available. I would think that even though wind dispersal is possible, it would be rare that successful landing on a suitable dung substrate would occur.

Liverworts

Schuster (1966) considered liverwort dehiscence and spore dispersal to be timed to occur when there would normally be strong, drying winds to dry the outer layer of the capsule wall, causing the valves to curl backward. Since outer walls would dry first, they would be more contracted than inner walls.

Liverworts are aided in spore dispersal by elongate structures with spiral thickenings called **elaters** (Figure 11). These respond to changes in moisture, causing walls of cells between spirals to contract, thus resulting in twisting of elaters and contortion or bending of cells. When the elater reaches a certain point of tension due to remaining water adhering to walls of drying cells, it suddenly releases the remaining water and jerks into its original shape, thrusting nearby spores into the air. There are variations on this theme, discussed in the subchapter on Marchantiophyta. Schuster (1966) considers that in liverworts, numerous small spores (6-18 μm in diameter) are an adaptation for wind dispersal.

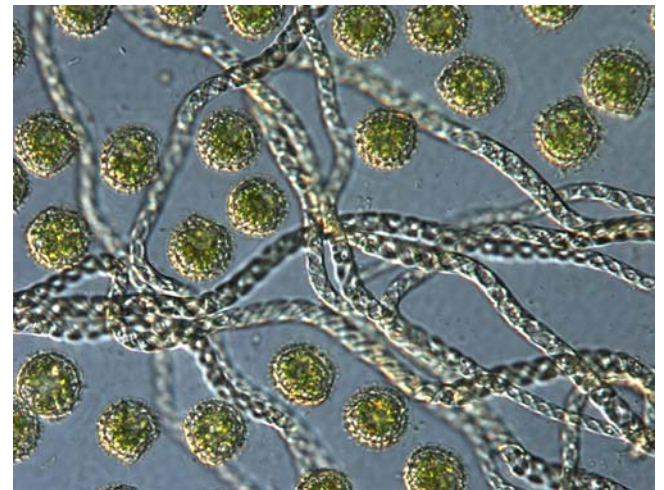


Figure 11. *Hymenophyton* sp. spores and elaters. Photo by Karen Renzaglia, with permission.

Invasive Species

The invasive *Campylopus introflexus* (Figure 12) has spread rapidly over Europe, apparently by its small spores (Hassel & Söderström (2005). Once there, it spreads rapidly by programmed fragmentation of deciduous leaves. *Orthodontium lineare* (Figure 13), another invasive species in Europe, spreads by numerous small spores. It lacks vegetative reproduction, although its ability to grow from fragments remains to be tested. Because it must establish and spread by spores, it requires about thirty years

before it is able to produce mature spores; *Campylopus introflexus* requires only ten. It appears that the spread of spores in both species is predominantly (or entirely) by wind.



Figure 12. *Campylopus introflexus*, an invasive weed in Europe. Photo by Michael Lüth, with permission.



Figure 13. *Orthodontium lineare*, an invasive species in Europe. Photo by Michael Lüth, with permission.

Decay Dispersal

Some capsules lack peristome teeth and do not dehisce (**cleistocarpous capsules**; Figure 14-Figure 17). In these cases, the capsule must decay or be eaten for spores to escape.



Figure 14. *Goniomitrium enerve* with cleistocarpous capsules. Photo by David Tng, with permission.



Figure 15. *Physcomitrella patens* cleistocarpous capsule. Note neck of archegonium forming a dark projection at the tip of the calyptra. Photo through Wikimedia Commons.

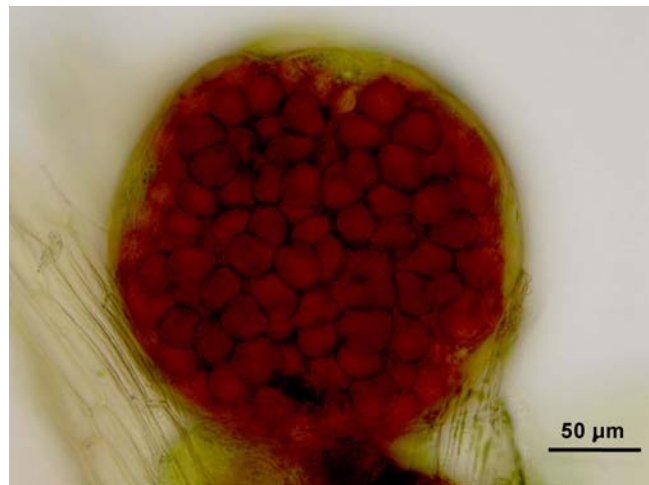


Figure 16. *Micromitrium synoicum* cleistogamous capsule. Photo from Duke University Herbarium, through Creative Commons.

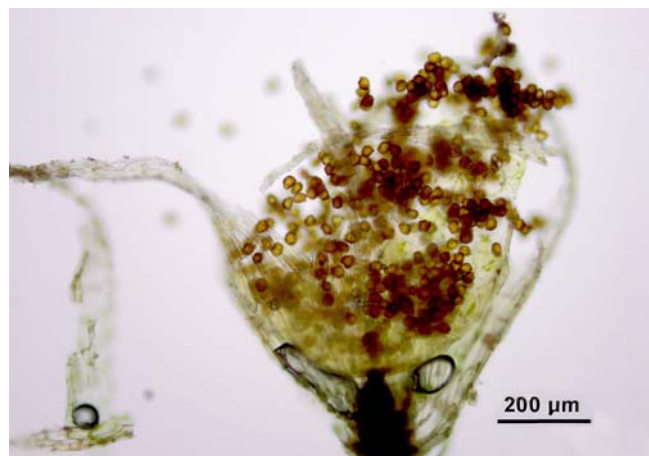


Figure 17. *Micromitrium synoicum* cleistogamous capsule breaking apart, showing spores. Photo from Duke University Herbarium, through Creative Commons.

Even some capsules with an operculum and peristome may use decay as a means of releasing spores. In *Fontinalis novae-angliae* (Figure 18) and *F. dalecarlica* (Figure 19), abrasion by flowing water and debris (in New

Hampshire, USA) often erodes the capsule wall away with the operculum still intact. The capsules in this genus tend to be quite thick, perhaps an adaptation against premature erosion. But the question remains, are the spores still viable in these older capsules that seem to be heavily endowed with phenolics, or are these capsules that aborted before reaching the maturity needed for normal dehiscence and dispersal? Since these spores disperse in late winter, observations on the actual dispersal seem to be lacking, my own included.

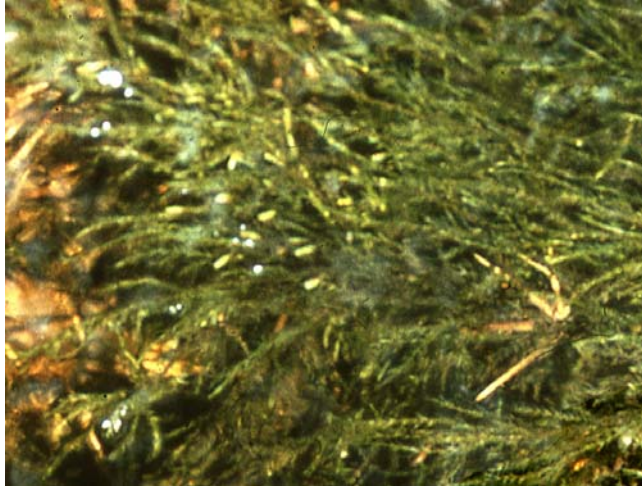


Figure 18. *Fontinalis novae-angliae* with capsules. Photo by Janice Glime.



Figure 19. *Fontinalis dalecarlica* with capsules. Photo by Janice Glime.

I have observed capsules in these two species, still submersed, but not yet mature. Korsteli (2003) observed very different behavior in *Fontinalis antipyretica* (Figure 20) from the dense capsule walls I observed after spring runoff. He reported that sporophytes in this species are produced under water, but that dry conditions were needed for the capsule to dehisce. Under such conditions, the operculum tears loose, lifted by hygroscopic movements of the exostome teeth. Spores are released by reversible changes in the shape of the capsule! Misha Ignatov (Bryonet 29 March 2013) observed the teeth in the lab and watched them gyrate as they dried (Figure 21).



Figure 20. *Fontinalis antipyretica*. Photo courtesy of Betsy St. Pierre.

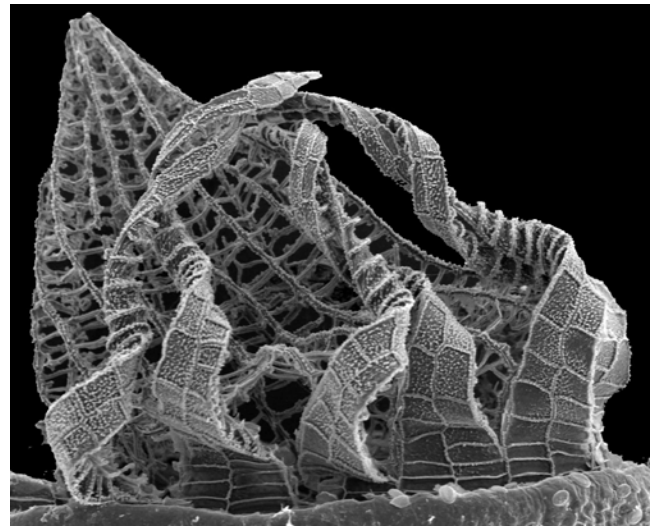


Figure 21. *Fontinalis* sp. peristome (SEM) showing the contorted teeth as they dry. Photo by Misha Ignatov, with permission.

Buxbaumia aphylla (Figure 22) seems to disperse its spores more commonly by having the capsule split across the broad, flat upper surface. The capsule wall peels back, exposing the spores (Figure 22). In my observations, this appears to be the typical case – I have not found capsules with intact walls and exposed teeth, the condition one would expect for dispersal through the capsule opening. In fact, my early observations led me to think these capsules were being eaten, but careful periodic observations by my graduate student, Chiang-Liang Liao, proved me wrong. Nevertheless, once the spores are exposed, it appears some insects may indeed feed on them and potentially disperse them. Müller (2012) found that adult fungus gnats (Mycetophilidae; Figure 23) in Germany feed on these spores (Figure 23-Figure 24) and thus might carry spores on their bodies, consequently dispersing them.



Figure 22. *Buxbaumia aphylla* showing the peeled back capsule wall that exposes the spores. The lower capsule has lost its operculum and the teeth are showing. Photo by Janice Glime.



Figure 23. *Buxbaumia aphylla* with fungus gnats eating spores from the few remaining capsules. Photo by Jörg Müller, with permission.



Figure 24. *Buxbaumia aphylla* capsules partially eaten by fungus gnats. Photo by Jörg Müller, with permission.

It may surprise the novice to find that in the fly-dispersed family Splachnaceae exist non-fly-dispersed species that require capsule decay for release of spores from the capsules. In these species, there are no teeth and the capsule does not dehisce. Among these are *Voitia nivalis* (see Figure 25) (Goffinet & Shaw 2002) and *Tayloria callophylla* on soil (Figure 26); others are epiphytic except for two additional coprophilous but cleistocarpous (capsule not opening) species.



Figure 25. *Voitia hyperborea* in Svalbard, showing cleistocarpous capsules. Photo by Michael Lüth, with permission.

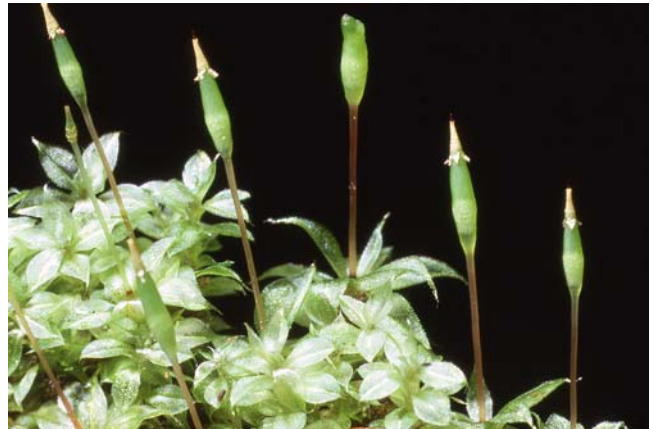


Figure 26. *Tayloria callophylla* with capsules, from New Zealand. This is a species that occurs on soil and lacks the expanded hypophysis typical of *Splachnum*. Photo by Zen Iwatsuki, with permission.

Carrión *et al.* (1995) cite xerophytic *Phascum* spp. (Figure 27), *Pterygoneurum* spp. (Figure 28), and *Acaulon* (Figure 29) as sharing cleistocarpous capsules, large spore size, and highly sculptured spores. But interesting anomalies exist. *Pterygoneurum sampaianum* (Figure 30) has two spore sizes and spore wall thicknesses. Carrión *et al.* suggest this permits most germinations to occur in suitable habitats of parents while allowing for at least some longer transport to new locations. Vitt (1981) surmised that cleistocarpy was important in ephemeral habitats, where large spores have a better chance of surviving until the conditions become favorable again. Having two types of spores would be advantageous in these conditions.

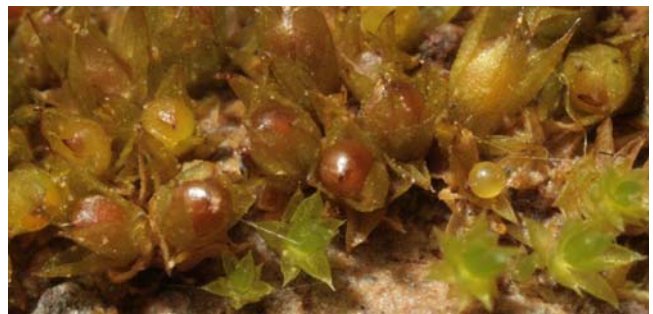


Figure 27. *Tortula acaulon* (= *Phascum cuspidatum*) with cleistocarpous capsules. Photo by Jan-Peter Frahm, with permission.



Figure 28. *Pterygoneurum ovatum* with ovate capsules. Photo by Kristian Peters, with permission.



Figure 29. *Acaulon triquetrum* with cleistocarpous capsules. Photo by Michael Lüth, with permission.



Figure 30. *Pterygoneurum sampaiianum* in sand, a species with two spore sizes. Photo by Jan-Peter Frahm, with permission.

Surely through such a long period of evolution some of these cleistocarpous capsules must have evolved invertebrate partners that help in the destruction of the capsule wall. Or is it bacteria, or fungi, that do the deed? But certainly some open as a result of torque resulting from drying.

Animal Dispersal

Volk (1984) considered animals to be the most important means of dispersal for the **Marchantiales** in Namibia, suggesting that dispersal was facilitated by the spore ornamentation.

When we think of animal dispersal, we think of "velcro" plants that attach their propagules by small hooks to the fur of their host, or we think of seeds passing through

the digestive tract unharmed while the host benefits from the surrounding fruit. But are bryophytes too small to utilize such large animal carriers? Are capsules good substitutes for fruits? We must think on a small scale, and the obvious disperser seems to be insects, those creatures upon which the pollen grain must so often depend. But most people know only about the ability of the **Splachnaceae** to hitch a ride on an unsuspecting insect, the fly, to achieve the dispersal of their spores. It appears we have been missing something.

Earthworms

As earthworms pass soil particles through the gut, they also transport bryophyte diaspores. Van Tooren and During (1988) found that spores were more successful at germination than vegetative diaspores when taken from earthworm castings (Figure 31). Interestingly, During (1986) found that spores from more than 1 cm down were more likely to germinate than those in the first centimeter. He suggested a higher mortality rate among those in the first centimeter, or that most of the spores were washed down to deeper layers. It is likely that a spore in that first cm would get enough water and light to effect germination, but that they might not remain wet enough, or have enough light, to survive after germination; they might also get water frequently, activating respiration, but having insufficient light to germinate, thus losing considerable energy each time they get wet. Nevertheless, it is also a good hypothesis that many got washed down to lower layers.



Figure 31. Earthworm castings, a potential means of bringing bryophyte diaspores to the surface. Photo by Muhammad Mahdi, through Creative Commons.

Gange (1993), examining primarily fungal spores, found that earthworm castings had higher concentrations of spores than did the surrounding soil. If they likewise concentrate bryophyte spores, this could be an effective dispersal mechanism, perhaps placing diaspores into the diaspore bank, or removing the diaspores from the diaspore bank, despite the high mortality rate seen by Van Tooren and During (1988). A high mortality is not 100%, so those spores that do survive might be effective in later establishment.

Insects and Spiders

It is likely that arthropods such as insects and spiders have a greater role in bryophyte spore dispersal than we

had imagined. Such characteristics as hairs on the arthropod or sticky spores facilitate such dispersal.

Ignatov and Ignatova (2001) report that small spiders, mites, and beetles that walk among the cave moss (*Schistostega pennata*) (Figure 86) plants become "more or less dirty" with spores. Smooth-bodied insects seem to be poor carriers, but hairy arthropods such as spiders, especially *Trochosa* spp. (Figure 32), and harvestmen (*Opiliones*) are more likely to carry the sticky spores.



Figure 32. *Trochosa spinipalpis*, a hairy spider that might contribute to dispersal of sticky spores. Photo by Jørgen Lissner, with permission.

Schuster (1966) reports observing lathridiid beetles feeding on spores of the leafy liverwort *Lophozia porphyroleuca*, but alas, that was in a herbarium. In fact, one of the bits of "evidence" often cited to say that bryophytes are inedible is the lack of dermestid beetles found in bryophyte herbaria, whereas seed plants must be stored with mothballs if we don't want them to disappear into the guts of these beetles. But this one observation of a lathridiid beetle eating liverwort spores does not prove that they ever disperse them in nature, or for that matter, even eat them in nature. On the other hand, this family of beetles is known to eat fungal spores, digest the exine, and disperse them in viable condition from the other end of the gut. So maybe...

Ants

A somewhat more believable story, but one Schuster (1966) considers least credible, is that Szepesfalvy considers ants to disperse spores of the liverwort *Athalamia hyalina* (Figure 33) because ants use spores (Figure 34) as food (Loria & Herrnstadt 1980) and these spores are often found injured. Based on this evidence, it is likely that some are also dispersed unharmed.



Figure 33. *Athalamia hyalina*, a liverwort that serves as food for ants. Photo by Adolf Ceska, with permission.

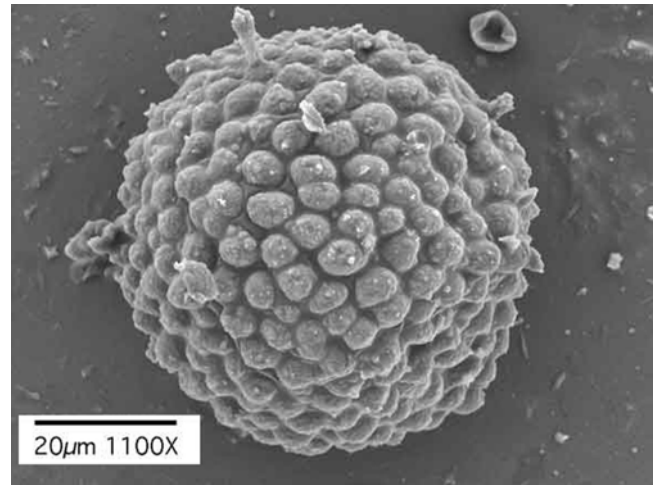


Figure 34. *Athalamia hyalina* distal spore wall SEM. Photo by William T. Doyle, with permission.

Rudolphi (2009) considered that the ant *Lasius platythorax* might be a passive dispersal agent of the asexual propagules of the moss *Aulacomnium androgynum*. Both the moss and the ants occur on dead wood in Swedish forests. Experiments showed that 33% of the ants has gemmae adhering to them within less than two minutes of exposure to the mosses. Half of these gemmae continued to adhere to the ants for approximately 4 hours, indicating that the ants could be effective dispersal agents.



Figure 35. *Lasius platythorax*, dispersal vector for gemmae of *Aulacomnium androgynum*. Photo by April Nobile, <www.antweb.org>, through Creative Commons.



Figure 36. *Aulacomnium androgynum* showing clusters of gemmae. Photo by Des Callaghan, with permission.

Aquatic Insects

Even aquatic insects may contribute to dispersal. Revill *et al.* (1967) cultured the flora and fauna occupying the surfaces of four aquatic Diptera [*Tipula triplex* (see Figure 37), *Bittacomorpha clavipes* (Figure 38), *Chaoborus punctipennis* (see Figure 39), *Chironomus* sp. (as *Tendipes*; Figure 40)]. Using 51 cultures from washings, they found algae, protozoa, Cyanobacteria, and moss protonemata. *Bittacomorpha clavipes* carried significantly more of these organisms than the other three species.



Figure 37. *Tipula abdominalis* larva. Photo through Creative Commons.



Figure 38. *Bittacomorpha clavipes* adult. Photo from William Vann at Edupics, free for educational use.



Figure 39. *Chaoborus flavicans* larva at water surface. Photo by Malcolm Storey (DiscoverLife), through Creative Commons.



Figure 40. *Chironomus* larva. Photo by Gerard Visser <www.microcosmos.nl>, with permission.

Sticky Spores

Ignatov and Ignatova (2001) found that spores of *Schistostega pennata* (Figure 41-Figure 42) were covered with a sticky substance, much like spores in the *Splachnaceae* (Figure 43-Figure 46). This substance causes many spores to stick together and prevents effective transport by wind. On the contrary, the spores are better adapted to transport by arthropods and other animals to which they adhere. Although Gaisberg and Finckh (1925) reported their inability to be transported by wind, commenting that they are glued together and are dispersed through animals, it appears that most bryologists have paid little attention to the sticky nature of the spores or their mode of transport until the publication of Ignatov and Ignatova in 2001.

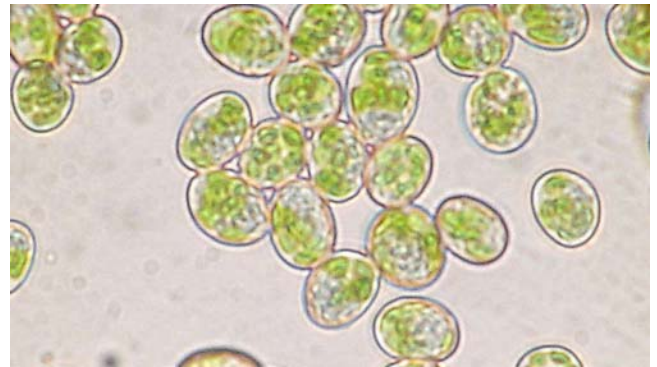


Figure 41. Elliptical spores of *Schistostega pennata* demonstrating tendency to stick together. Photo by Misha Ignatov, with permission.

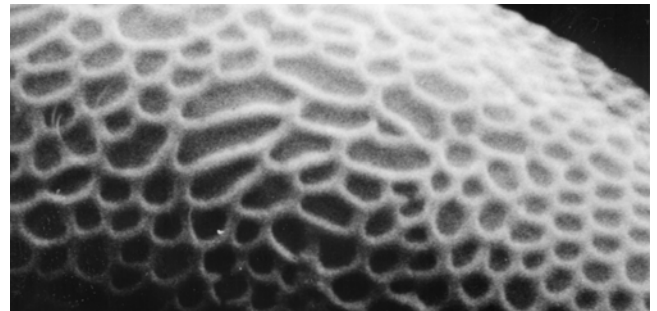


Figure 42. SEM image of spore surface of *Schistostega pennata* showing sticky perine. Photo by Misha Ignatov, with permission.

The *Schistostega pennata* sporophyte (Figure 86) shares another unique character with *Splachnaceae* (cf. Koponen 1990); its seta continues growth after the capsule has opened. But it also shares with liverworts the habit of producing its capsule before the seta elongates. In fact, it may even lose its operculum before elongation begins. The seta itself is unique, having long-rectangular, thin-walled

cells with round chloroplasts scattered in such a way that the seta appears to have be fluorescent.

Using sticky tape to trap insects near *Schistostega pennata*, Ignatov and Ignatova (2001) found spores, probably of *S. pennata*, adhering to adult members of the fly family **Dolichopodidae**. They also found that some ants (*Formica rufa*) and beetles (*Geotrupes stercorarius*; Figure 90) climbed among the *S. pennata* and that the beetles carried spores of this species.

Even the elliptical spore shape is unusual, characterizing both *Schistostega* (Figure 42) and the **Splachnaceae**. This shape increases the surface area relative to volume, making attachment easier. Demidova and Filin (1994) have suggested that the light green color of the bulk of spores contrast to the deeply colored ones near the top of the capsule in this species and **Splachnaceae**. They suggest that these light-colored spores would also help attract insects. The autoicous sexual condition (but with separate male and female plants originating from the same protonema and thus from one spore) insures that both sexes will be available (Ignatov & Ignatova 2001). [Note that many bryologists consider this a dioicous condition because the male and female shoots are different; whichever interpretation or term is used, this presents a special case.]

Muscidae and Dung Mosses

The same nomenclatural problem of separate sexes arising from one protonema exists for *Splachnum rubrum* (Figure 43) and *S. luteum* (Figure 44). The family **Splachnaceae**, discussed also in the chapter on nutrients and Terrestrial Diptera, is the only other group of bryophytes considered to be specially adapted for animal dispersal. The oldest report seems to be that of Bryhn (1897), reporting that flies visited *Splachnum rubrum* (Figure 43) and carried the spores to fresh dung. Wettstein (1921) expanded on this observation, verifying dispersal by flies in additional species in the family. Since then, A Koponen, T. Koponen, Cameron, and Marino, among others, have studied this fascinating family extensively, demonstrating not only that flies carry the spores, but determining the attractants.

Among the 73 species in this family, approximately half are **entomophilous**, being dispersed by flies (Diptera) (Erlanson 1930; Koponen & Koponen 1978; Goffinet *et al.* 2004; Marino *et al.* 2009). These same species are **coprophilous**, growing on feces or carrion. Their capsules are often brightly colored and are known to attract flies through their scent, which typically mimics that of decaying organic matter. The relationship between the fly and the moss is typically species-specific, with the capsules producing a unique odor as its attractant. Furthermore, it is the sporophytes that produce the odors (Erlanson 1930; Pyysalo *et al.* 1978, 1983; Marino *et al.* 2009), with the gametophytes being nearly odorless. Interestingly, there was an inverse relationship between the size of the **hypophysis** and the strength of the odor (Marino *et al.* 2009), but perhaps this is an energy tradeoff.

In this family, the peculiar odor attracts the flies that subsequently walk about on the capsules and the spreading **hypophysis** (Figure 1), getting sticky spores (Figure 45) on their bodies, as in *Schistostega*. The flies are usually

attracted to both the dung substrate and the odor of the moss capsules. After investigating the capsules, the flies then travel to other dung, attracted to the odor of the wet dung, and deposit some of the spores as they wander about on the dung.



Figure 43. Capsules of *Splachnum rubrum*, showing the broadly expanded, umbrella-like hypophysis under the capsule. Flies are attracted to the iridescent red color and the odor, with the hypophysis providing a landing platform. Photo by Janice Glime.



Figure 44. *Splachnum luteum* with one of its fly dispersers sitting on the hypophysis. Photo from Biopix, through Creative Commons.

So why should such an elegant moss choose to live on something as unpleasant to humans as dung, and nowhere else? There seems to be no simple answer, so let's examine the facts. This parasol, modified in various ways among the species, is sterile tissue of the sporophyte. Perched atop the umbrella, like the knob to which the spokes of a wheel would be attached, is the capsule, housing the spores. The teeth differ in structure from those of most mosses (Koponen 1978, 1982) and are reflexed at maturity, exposing an open tiny canister of spores (Figure 45).



Figure 45. Capsule of *Splachnum ampullaceum* showing sticky spores with part of expanded **hypophysis** at base. Photo by Janice Glime.

This greatly expanded sterile tissue is the **hypophysis**, concealing a spongy tissue similar to a maple tree's mesophyll. The hypophysis itself is generally brightly colored in *Splachnum*, although somewhat more ordinary in other genera, and provides a landing platform for flies. In *Splachnum ampullaceum* (Figure 46) it is yellow to deep pink, and the plants are so crowded that if the colors don't attract your attention, the sheer numbers will. This of course also amplifies the odor. In *Splachnum rubrum* (Figure 43), the hypophysis is an iridescent purple-red, and I have to wonder if it reflects UV light, visible to some Diptera (Bishop 1974; Gerry *et al.* 2009), but not to us.

By this time, the dung is old and dry, emitting no more odor than the soil beneath, so it is not likely to attract would-be dispersers. However, since the moss has a "perfume" of its own (Erlanson 1930), emitting the unpleasantness of rotting food, sour or musty, from its hypophysis, it attracts the flies. Although these odors are generally faint to our insensitive noses, to a fly they are a virtual invitation. Steere (1958) describes some of the odors. *Tetraplodon* (Figure 50) smells of a strong acetic ester, *Splachnum sphaericum* (Figure 47) of lactic acid, and *S. luteum* (Figure 44) of a butyl compound. These chemicals (Table 2) include volatile octane derivatives and organic acids such as acetic, propionic, and butyric acids that are concentrated in the hypophysis (Koponen 1990).

When the capsule is moist, the columella, with a swollen end, serves as a plug after the operculum is shed. But on a dry day, the capsule contracts and the columella extrudes from the capsule, carrying upward with it clumps of spores exposed to the world. Instead of travelling by wind as individuals, typical of most other mosses, the spores of this moss clump together like the pollen of an

orchid, and apparently to the same advantage. They are picked up inadvertently on the hairs of flies (Koponen 1990; Eriksson 1992) exploring the odor and seeking reward. Once leaving the lure of the capsule, the fly, less discerning than a bee, is likely to be attracted to the odor of fresh dung, and hence carries the clumps of spores to their new home. But the story does not end there. It seems that the fly can even gain an advantage that insures its greater success. Scatophagids, the most frequent and effective of fly visitors, reputedly have greater copulatory success after visiting these mosses (Cameron & Wyatt 1986) – an aphrodisiac for flies!



Figure 46. *Splachnum ampullaceum* in southern Europe, showing the high density of sporophytes. Photo by Michael Lüth, with permission.

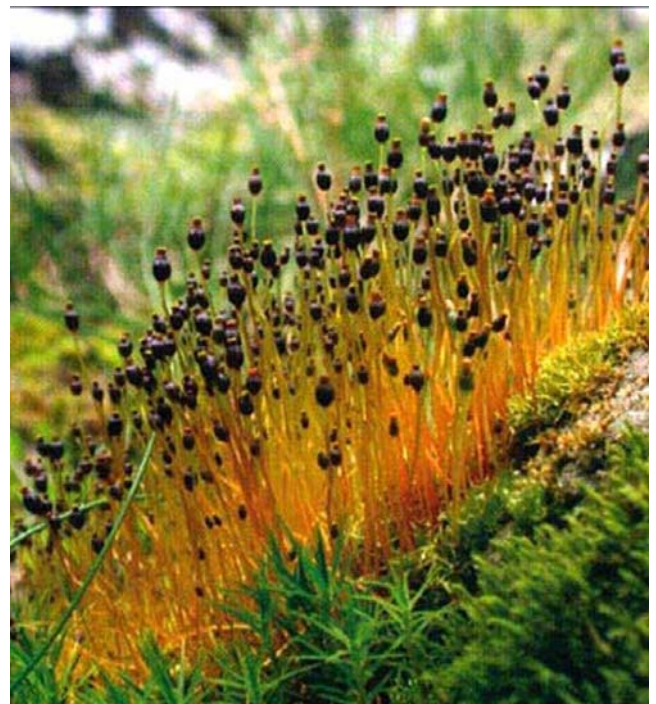


Figure 47. *Splachnum sphaericum* capsules, exhibiting a density that intensifies the lactic acid odor. Photo through Creative Commons.

Diversification of Spore Dispersal Strategy

The fly assemblages differ among individuals and among clumps of the **Splachnaceae** species. Koponen and Koponen (1978) experimented with attraction to **Splachnaceae** in Finland and demonstrated that different combinations of *Poliaetes lardarius* (Figure 48) and other dung flies were attracted to sticky traps baited with hidden sporophytes of *Splachnum ampullaceum* (Figure 46), *S. vasculosum* (Figure 49), and *Tetraplodon mnioides* (Figure 50). Marino (1991a) studied **sympatric** (having overlapping distributions) moss assemblages in central Alberta, Canada. Each moss species attracted 10-17 spore-carrying fly species, but visiting fly species assemblages differed by 77-92% among **Splachnaceae** species (Table 1). Furthermore, the Diptera species captured on the dung were less diverse than those captured from the capsules of the mosses (Marino 1988; 1991b). Marino (1991a) concluded that species-specific recruitment of fly guilds appears to result from differences in attraction to sporophytes through distinct odors created by the moss (especially the capsules), visual cues, or combinations of these.



Figure 48. *Poliaetes lardarius* side view, a dung fly attracted to *Splachnum ampullaceum*. Photo by Richard Bartz, through Wikipedia Commons.

Table 1. Mean (± 1 S.D.) number of spores ($\times 10^3$) carried by fly species trapped on 4 species of mosses in a trapping experiment at Ft. Assiniboine, Alberta. The number of flies carrying spores is shown in parentheses. Fly species in which only a single individual carried spores are not shown (Marino 1991b).

Fly Species	Moss species			
	<i>Tetraplodon angustatus</i>	<i>Tetraplodon mnioides</i>	<i>Splachnum ampullaceum</i>	<i>Splachnum luteum</i>
<i>Eudasyphora cyanocolor</i> Zett.	74 \pm 100 (13)	29 \pm 17 (10)		24 \pm 30 (2)
<i>Helina cothurnata</i> Rondani	52 \pm 39 (11)			
<i>Phormia terrae-novae</i> R.D.	16 \pm 5.3 (2)	20 \pm 20 (9)		
<i>Scatophaga furcata</i> Say	26 \pm 27 (6)		32 \pm 22 (6)	16 \pm 24 (9)
<i>Calliphora vomitoria</i> L.		46 \pm 50 (11)	29 \pm 12 (3)	16 \pm 13 (4)
<i>Pegoplata patellans</i> Pand.			23 \pm 19 (26)	14 \pm 14 (18)
<i>Phormia regina</i> Meigen		42 \pm 50 (4)		
<i>Ravinia</i> sp. 1		6.2 \pm 1.8 (6)		12 \pm 9.1 (16)
<i>Sepsis</i> spp.	5.8 \pm 3.8 (3)			
<i>Cynomyopsis cadaverina</i> L.		30 \pm 27 (7)		
<i>Hydrotae meteorica</i> L.		17 \pm 7.7 (7)		
<i>Muscina assimilis</i> Fallen		20 \pm 8.2 (4)		
<i>Lucilia</i> sp. 1		23 \pm 13 (4)		
<i>Fannia spathiophora</i> Mall.		24 \pm 35 (3)		
<i>Pegohylomyia</i> sp. 1		14 \pm 12 (2)		
<i>Mydaea</i> sp. 1			25 \pm 23 (5)	
<i>Scatophaga suilla</i> Fab.			29 \pm 22 (5)	
<i>Hebecnema nigricolor</i> Fallen			40 \pm 48 (5)	
<i>Hydrotae militaris</i> L.			45 \pm 65 (3)	
<i>Phaonia curvipes</i> L.			15 \pm 14 (2)	
<i>Polietes orichalceoides</i> Huck.			69 \pm 19 (2)	
<i>Myospila meditabunda</i> Fab.				3.5 \pm 2.2 (5)
<i>Pegoplata nigriscutellata</i> Stein				6.2 \pm 1.8 (2)
<i>Hydrotae scambus</i> Zett.				3.7 \pm 1.8 (2)
<i>Hylomyza partita</i> Meigen				6.2 \pm 1.8 (2)
Total	(37)	(63)	(59)	(60)

Table 2. Volatiles detected in the hypophysis and urn of five members of **Splachnaceae**. From Koponen *et al.* 1990. Indications for *Aplodon wormskioldii* based on Pyysalo *et al.* 1983.

	<i>Splachnum luteum</i>	<i>Splachnum vasculosum</i>	<i>Splachnum sphaericum</i>	<i>Aplodon wormskioldii</i>	<i>Splachnum rubrum</i>
Octanal	-	-	X	-	X
3-Octanone	X	-	X	-	-
3-Octanol	-	X	X	X	-
Trans-2-octenal	-	X	X	X	-
1-Octen-3-ol	X	X	X	X	X
1-Octenol	X	X	X	X	-
2-Octen-1-ol	-	X	X	-	-
2-Octenol	-	-	X	-	-
2-Ethyl-hexanal	-	-	X	-	-
Phenylacetylene	-	-	X	X	-
Benzyl alcohol	-	-	X	-	-
Phenole	X	-	X	-	X
Cyclohexycarboxylic acid	-	X	-	-	-
Phenethyl alcohol (2-phenyl ethanol)	-	-	-	-	X
Phenylacetic acid	-	X	X	X	X
Acetic acid	-	-	X	X	-
Propionic acid	-	-	X	X	-
Butyric acid	-	-	X	X	-
Valeric acid	-	-	X	X	-
Caproic acid	-	-	X	X	-
Benzoic acid	-	-	X	X	-
Phenylacetic acid	-	-	X	X	-
Palmitic acid	-	-	X	X	X

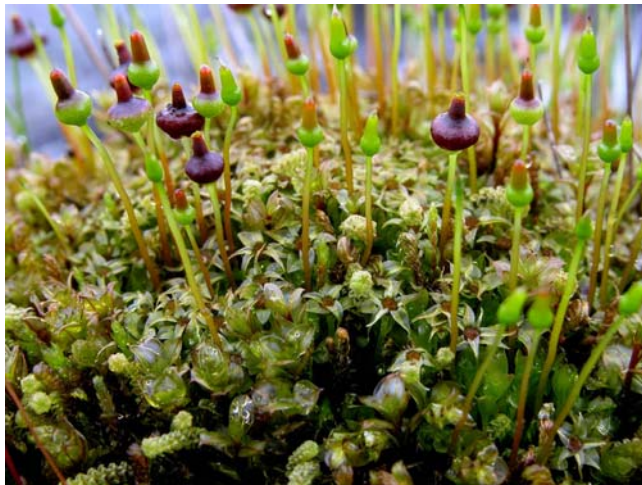


Figure 49. *Splachnum vasculosum* capsules and male splash platforms. Photo by Dick Haaksma, with permission.

Cameron and Wyatt (1986) studied dispersal for *Splachnum ampullaceum* (Figure 46), *S. rubrum* (Figure 43), *S. sphaericum* (Figure 47), *S. vasculosum* (Figure 49), and *Tetraplodon mnioides* (Figure 50) and found that the fly family Scatophagidae (*Scatophaga*; Figure 51) was both the most frequent and most effective visitor to the moss colonies. Other visitors included *Delia* (Anthomyiidae), *Myospila* (Muscidae; Figure 52), and *Eudasyphora* (as *Pyrellia*; Muscidae; Figure 53). They further demonstrated that wind is not an effective dispersal agent for these species.



Figure 50. *Tetraplodon mnioides* capsules. Photo by Zen Iwatsuki, with permission.



Figure 51. *Scatophaga stercoraria*, member of a genus that visits **Splachnaceae** capsules. Photo by Luc Viatour <www.Lucnix.be>, through Creative Commons.



Figure 52. *Myospila mediatubunda*, member of a genus that visits **Splachnaceae**. Photo by Valter Jacinto, through Creative Commons.



Figure 53. *Eudasyphora cyanicolor*, a carrion fly. Photo by Tristram Brelstaff, through Creative Commons.

Troilo and Cameron (1981) consider the transport of spores in the *Splachnum ampullaceum* (Figure 46) by flies [*Eudasyphora* (as *Pyrellia*) *cyanicolor* (Figure 53)] to be passive. This fly species oviposits on carrion, but it will use dung when carrion is not available, whereas *S. ampullaceum* grows almost exclusively on dung. The moss capsules attract them, and if they are chased away, they quickly return. The capsule is adapted by its bright colors, expanded hypophysis that serves both to attract and as a landing platform, a dung-like odor, teeth that extend outward, and a shrinking capsule that forces the adhesive spores outward. Cameron and Troilo (1982) added to this story by documenting that landing by *Eudasyphora cyanicolor* flies demonstrated a 20-fold preference for yellow-colored disks over blue or red disks placed among sporophytes of *S. ampullaceum* in Michigan, USA, suggesting the spore dispersal may not be passive after all. In fact, they never visited the red disks. This is an interesting observation and begs further investigation. Flies are typically attracted to red (don't wear red in mosquito or blackfly season!). And *S. ampullaceum* typically has a mix of yellow and pinkish red capsules (Figure 1). On the other hand, pink flowers do not usually attract flies.

The most activity of *Eudasyphora* (**Muscidae**; Figure 53) on the capsules was on warm days when the odors were strongest (Troilo & Cameron 1981). The moss is a successful odor mimic, as demonstrated by fly visits that equalled those to carrion and exceeded those to a protein source or fly medium (Figure 54). But once there, the visit to the moss capsule was significantly shorter than visits to carrion or protein substitute. Moreover, the flies never exhibited feeding behavior on the capsules, only sampling behavior. Troilo and Cameron consider this to be a **commensal** relationship in which the moss benefits from dispersal but the flies are neither benefitted nor harmed. One could argue that the moss is being a parasite by taking energy from the flies and using it for dispersal while providing nothing in return, but others have argued that the flies may get the benefit of increased mating opportunity.

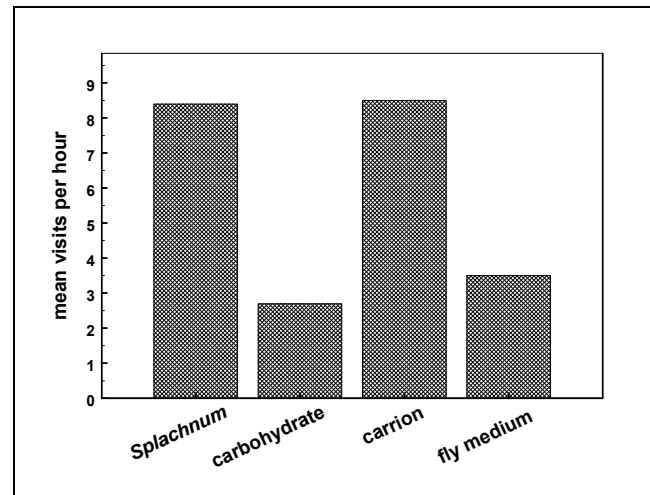


Figure 54. Mean number of visits by the carrion fly *Eudasyphora cyanicolor* (Figure 53) on *Splachnum ampullaceum* (Figure 46) and three nutritional substrates. Note that there was no evidence of feeding on *S. ampullaceum*. Graph based on table from Troilo & Cameron 1981.

Many of the fly species associated with the **Splachnaceae** studied by Marino (1991b) are anthomyiids. By mimicking the flower and odor cues typically used by the adult **Anthomyiidae**, a family with seed predators and pollinators, the mosses have achieved what appears to be a very effective means of spore dispersal.

This very targeted means of dispersal may be a tradeoff between energy needed for attraction and that needed for spore production (Marino 1991a). These species have fewer spores **and** smaller spores than most mosses. This high energy requirement may account for the evolution from a specialist such as these entomophilous species to the generalist strategy of the coprophilous species such as *Tetraplodon paradoxus* (Figure 55), and the two *Voitia* species (**Voitioideae**; Figure 56) that lack sporangial dehiscence. In *Tayloria* (Figure 57), both anemophilous and entomophilous species exist.



Figure 55. *Tetraplodon paradoxus*, a species with indehiscent capsules. Photo by Michael Lüth, with permission.



Figure 56. *Voitia nivalis* with capsules. Photo by Michael Lüth, with permission.

It appears that the dung habitat may provide another significant role. One advantage to this dispersal type is that it ensures that both male and female spores will arrive at the same site. In populations of *Tayloria tenuis* (Figure 57) on cattle droppings in the Eastern Pyrenees, the protonemata are at first the only conspicuous stage (Lloret 1991). The plants are clustered and despite high mortality, the entire dung substrate is soon covered with protonemata. Within 1-2 years the leafy plants develop and ultimately produce capsules. These capsules are often numerous, as seen in *Splachnum ampullaceum* (Figure 46). This is in part due to the female:male ratio of 2:1, at least in the *Splachnum* species [*S. ampullaceum* (Figure 46), *S. sphaericum* (Figure 47), *S. rubrum* (Figure 43)] of Isle Royale, Michigan, USA (Cameron & Wyatt 1990). But in experiments, environmental conditions can alter this ratio, with low light, pH, and nutrients favoring the production of males.

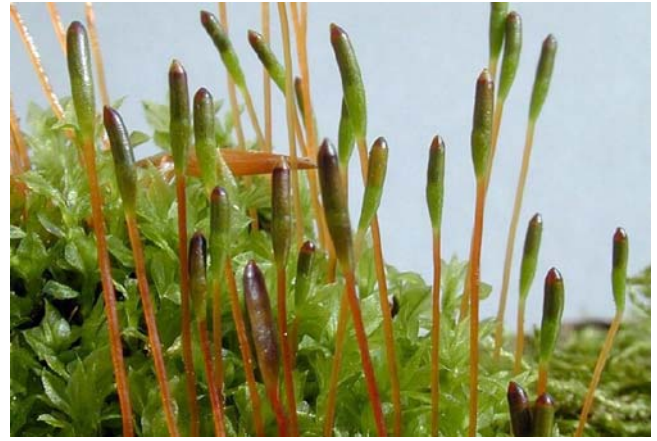


Figure 57. *Tayloria tenuis* with capsules, a species that grows on dung. Photo by Michael Lüth, with permission.

In *Splachnum ampullaceum* (Figure 46), males and females can arise from the same protonema, ruling out any bias in dispersal of spores. For this high degree of fertilization success, dispersal of the sperm to the female benefits from the density of the plants. Cameron and Wyatt (1990) found that the average sperm dispersal distance is less than 5 mm. This proliferation of sporophytes is reminiscent of the Asteraceae, acting as a single unit through the clumping of so many capsules. Furthermore, the early period of establishment has served to eliminate weak genotypes among the protonemata, although there is no guarantee that these same weaknesses would occur among the leafy plants.

As the capsules mature, that moist and smelly dung that once attracted the flies becomes dry and looks more like a cardboard Frisbee, or in the case of moose dung, like a clump of well-done toasted marshmallows. Nevertheless, once spores are sent upon their way, the remaining plants are soon covered by larger pleurocarpous mosses that are typical of the forest soil. This is an ephemeral habitat for the **Splachnaceae**.

All of this attraction is costly, requiring energy to produce the hypophysis and make volatile attractants. To maintain this, the mosses are able to access the higher concentrations of N, P, and Ca that occurs in dung (Webster 1987). Meanwhile, most other mosses typically die in areas with such high nitrogen concentrations resulting from manuring (Geissler 1982). There have also been suggestions that the growth of the protonemata may be promoted by substances such as Gibberellic Acid produced by accompanying fungi (Von Maltzahn & MacQuarrie 1958; Vaarama & Tarén 1959).

Cameron and Wyatt (1986) have suggested that the **Splachnaceae** requirements for dung may actually be a requirement for their fly dispersers, and the flies travel from one dung heap to another. There seems to be an interesting correlation between means of dispersal and substrate that supports this hypothesis. As noted earlier, all of the **entomochorous** (i.e. requiring insect dispersal) species are also **coprophilous** (living on dung or corpses); the **anemochorous** (wind-dispersed) species are **humicolous** or epiphytic (Goffinet & Shaw 2002). In the subfamily **Voitioideae**, three taxa are coprophilous but cleistocarpous (capsule not opening), lacking a peristome and dispersing spores only after the sporangial wall disintegrates.

Flies are not restricted to landing on dung, to any particular moss species, or to any particular habitat (Marino 1986), so this diverse behavior would seem to limit successful dispersal. Nevertheless, spore success is typically very low among mosses, so even this hit-or-miss mechanism may be better than wind dispersal. And certainly it must be for these sticky spores.

In summary, Koponen (1990) considers three categories of adaptations of bryophytes for entomophily in the **Splachnaceae**:

- adaptations to a substrate of animal origin
- morphological adaptations
- chemical adaptations

In support of this, Koponen cites *Splachnum* (Figure 49) and the entomophilous species of *Tayloria* (Figure 61-Figure 62) as being restricted to the dung of herbivorous mammals. *Tetraplodon* (Figure 58-Figure 59) grows on skeletal remains, antlers, stomach pellets of predatory birds, or on dung. The entomophilous *Aplodon wormskioldii* (Figure 60) grows on corpses, on caribou (reindeer) dung, bones and antlers, on owl pellets, or on enriched gravel.



Figure 58. *Tetraplodon angustatus* with capsules on caribou antler at Jasper, Canada. Photo by Janice Glime.

Those of us in the Northern Hemisphere are familiar with this fascinating family of mosses largely because of their ability to attract flies, but in the Southern Hemisphere, such attraction does not exist, or does it?! Mighell (2011) investigated *Tayloria mirabilis* (Figure 61-Figure 62), a South American endemic, because it had been suspected of having fly dispersal. They trapped 218 flies over the plants on dung and found that 63 of them had spores of *T. mirabilis*. The flies comprised seven species from Muscidae and Calliphoridae. Furthermore, germination of the transported spores were 46.7% successful; identity of the spores was verified by DNA analysis. This example becomes more interesting when we realize that the plants (and flies) are associated with more than one kind of forest dung and that all the current large forest mammals there are exotic! Rapid evolution or pre-adaptation?



Figure 59. *Tetraplodon angustatus* with capsules on caribou skull at Jasper, Canada. Photo by Janice Glime.



Figure 60. *Aplodon wormskioldii* with capsules in Svalbard. Photo by Michael Lüth, with permission.



Figure 61. *Tayloria mirabilis* capsules, a species that attracts flies in the Southern Hemisphere. Photo by Jan-Peter Frahm, with permission.



Figure 62. *Tayloria mirabilis* capsules and fly near Cape Horn, Chile. Note the spores on the front leg and around the eye. Photo by Adam Wilson, through NYBG public domain.

In the same year, Jofré *et al.* (2011) reported a second example of fly-attracting Splachnaceae in the Southern Hemisphere. This time, it was *Tayloria dubyi* (Figure 63) growing on bird dung in the subAntarctic region of Cape Horn, Chile. The bird dung appears to be exclusively that of the Snow Goose *Chloephaga picta* (Figure 64). When Jofré Acevedo (2008) germinated the spores in the lab, they grew much better on snow goose dung than on horse or cattle dung. *Tayloria dubyi* releases its spores in the same months as the highest activity of Diptera (Jofré *et al.* (2010). Based on these findings, Jofré *et al.* (2011) trapped 64 flies, comprised of *Palpibracus chilensis* (Muscidae), *Dasyuromyia* sp. (Tachinidae), and an unidentified member of the Sarcophagidae, in traps above the sporophytes, but no flies appeared in traps above nearby *Sphagnum*, suggesting that *Tayloria dubyi* also attracts the flies.

Once we understood that flies were indeed attracted to the capsules of the Splachnaceae, not just (if at all) to the odors of the dung, work began to elucidate the attracting compounds. Koponen *et al.* (1990) identified 23 compounds in the hypophysis and urn among five Splachnaceae, demonstrating that the individual species were often unique. Data from the setae are not included here. The only volatile compound in the substratum was benzaldehyde, a compound not found in the capsules or setae.



Figure 63. *Tayloria dubyi* capsules, a Southern Hemisphere species of Splachnaceae that apparently attracts flies. Photo by Jocelyn Jofré., with permission.



Figure 64. *Chloephaga picta* (Snow Goose), potential bryophyte dispersal agents through the gut as well as feet and feathers. Photo by Fabien Dany <www.fabiendany.com>, through Creative Commons.

Molluscs

Could it be that slugs that consume capsules (Figure 65) do indeed carry spores to new locations? But alas, a slug by its very nature is slow, and such dispersal would not move the spores very far from home. Nevertheless, consumption can result in movement of spores to a new location, even if not very far away. But can they live?



Figure 65. Slug preying on capsules of *Leucolepis acanthoneuron*. Photo from Botany website, UBC, with permission.

Boch *et al.* (2013) tested the possibility that slugs could eat bryophyte spores, and that the spores could subsequently germinate. They fed capsules of four bryophyte species to three slug species. Overall,

approximately in half (51.3%) all 117 bryophyte samples fed to slugs, representing four bryophyte species [*Bryum pallescens* (Figure 66), *Funaria hygrometrica* (Figure 109), *Leptobryum pyriforme* (Figure 67), *Pellia endiviifolia* (Figure 68)], spores did germinate from feces. It is interesting that there was no difference between bryophyte species, but there were large differences among the three slug species (Figure 69). Spores from the feces of the slugs *Arion lusitanicus* (Figure 70) and *A. rufus* (Figure 71) had 76% and 74% success, respectively. Those from *Limax cinereoniger* (Figure 72), on the other hand, were only 12.9% successful. This mechanism would enhance the population size by moving spores away from the parent, but at the same time being more likely than wind dispersal to deposit them in places where they can grow successfully. Türke *et al.* (2013) found that slugs could transport seeds in the gut for 5 m, giving us an estimate of potential bryophyte dispersal distance.



Figure 66. *Bryum pallescens* with capsules, a species for which spores can be dispersed by slugs. Photo by David Holyoak, with permission.



Figure 67. *Leptobryum pyriforme* with capsules, a species for which spores can be dispersed by slugs. Photo by Michael Lüth, with permission.



Figure 68. *Pellia endiviifolia* males with reddish antheridial cavities and females in center. David Holyoak, with permission.

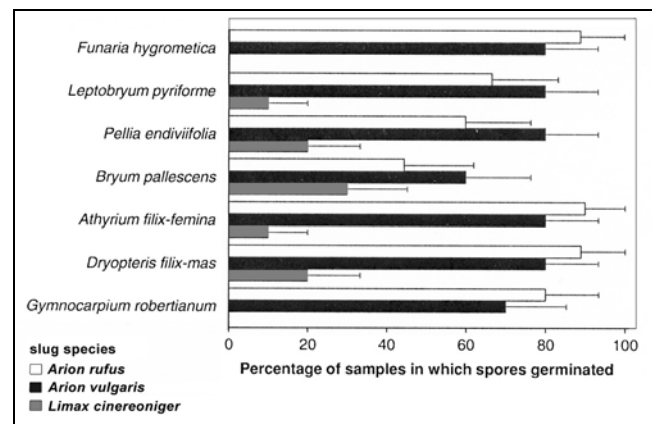


Figure 69. Germination percentages of bryophyte spores from feces of three species of slugs. Redrawn from Boch *et al.* 2013.



Figure 70. *Arion lusitanicus*, a species that disperses bryophyte spores through its feces. Photo by Håkan Svensson, through Wikimedia Commons.

In an experiment to determine success of spores that travelled through the digestive tract of slugs (*Arion* spp.; Figure 70), all plates containing eaten spores of *Mnium hornum* (Figure 73) and *Brachythecium rutabulum* (Figure 74) produced shoots, whereas only 80% of the plates with uneaten mature *Mnium hornum* spores and

70% of those with uneaten *Brachythecium rutabulum* spores produced shoots (Davidson 1989). Furthermore, the eaten spores showed little infection, suggesting some antibiotic property acquired from the digestive tract. Nitrogen, secreted in mucus and disposed in feces, may have enhanced the success of these spores.



Figure 71. *Arion rufus*, a species that disperse bryophyte spores through its feces. Photo by Walter Siegmund, through Wikimedia Commons.



Figure 72. *Limax cinereoniger*, a species in which most bryophyte spores died on the way through the digestive tract. Photo by Teemu Mäki, through Creative Commons.



Figure 73. *Mnium hornum*, a species whose spores are eaten by slugs in southern Europe. Photo by Michael Lüth, with permission.



Figure 74. *Brachythecium rutabulum* with capsules. Spores of this species are eaten by slugs. Photo by David Holyoak, with permission.

Using 11 species of mosses and 1 of liverworts, Boch *et al.* (2014) supported the concept that slugs can increase bryophyte establishment. They demonstrated that through their herbivory, the slugs reduce light competition, permitting a greater diversity of bryophytes to establish. Furthermore, the spores they ingest are able to germinate after passing through the digestive tract of the slug (**endozoochory**). After 21 days in an experimental setup, bryophyte cover was 2.8 times as high in enclosures with slugs that had previously been fed sporophytes when compared to enclosures with slugs that had not been fed sporophytes or with no slugs.

After 21 days the bryophyte cover was on average 2.8 times higher (3.9% versus 1.4%) and after eight months the bryophyte species richness 2.6 times higher (5.8 versus 2.2) in enclosures containing slugs previously fed with bryophyte sporophytes than in the other treatments. After 8 months, the increased vascular plant cover reduced the bryophyte diversity. Enclosures that had no seed sowing had 1.6 times as many bryophyte species compared to those receiving seeds.

But if we look further, we find that long distance travel by slugs and snails is indeed a possibility. Malone (1965) determined that fresh-water snails were able to attach to the feed of the killdeer (*Charadrius vociferus*) and travel there for sufficient time to accomplish overland dispersal, remaining alive. Adults of the snail *Lymnaea emarginata* could survive at least 14 hours. It is likely that other birds, both aquatic and terrestrial, could carry snails as well, providing considerable time for dispersal and making long-distance dispersal possible. And how long might the spores survive in a snail or slug eaten by a bird? Will those spores also be viable?

Fish

The ability of fish to transport bryophytes remains to be demonstrated. My student experimented with rainbow trout, known to strike at almost anything, to see if they would eat mosses in their attempts to remove aquatic insects. The student was unable to get the fish to attack the moving moss or eat it to get at insects. Finally, in desperation, he force fed it *Fontinalis duriaei* (Figure 75). Then he waited to collect the feces. The moss did appear in a cylindrical package of feces. It emerged in bright green

color and looked healthy. We put it in a jar of stream water from which the moss had been collected, kept it cold, and waited expectantly. Alas, the second day the *Fontinalis* was pale and appeared to be dead. No growth ever ensued.



Figure 75. *Fontinalis duriaei*, a species refused by rainbow trout and that does not survive in feces from force-fed fish. Photo by Michael Lüth, with permission.

Birds

Until recently, birds were barely considered as dispersers of bryophytes. Ducks are dispersers (Proctor 1959), but we have no idea how important they are. Spores of *Riella* (Figure 76; Tenge 1959) pass through the digestive tract of Mallards (*Anas platyrhynchos*; Figure 77) and remain viable (Proctor 1961). Assuming a mean residence time similar to that of seeds, which is about 7.5 hours, a migrating Mallard could move spores of this liverwort 20-30 km easily, and at times up to 1,400 km (Mueller & van der Valk 2002). It could, but does it?



Figure 76. *Riella cossoniana* showing sporangia (dark spheres) that can be dispersed by ducks. Photo by Jan-Peter Frahm, with permission.



Figure 77. *Anas platyrhynchos* (Mallards) female and male, potential dispersal vectors for aquatic bryophyte diaspores. Photo by Richard Bartz, through Wikimedia Commons.

Proctor (1961) suggested that the rarity of *Riella americana* may result from very specialized dispersal. Griffin (1961) found a large population of this species in a playa lake in Texas, USA, where its population measured 60 cm in width and approximately 1.7 km long. The production of gemmae may contribute to such large populations (Studhalter 1931). He examined 25 nearby similar lakes within a 25 km radius and could find no trace of the liverwort.

Following these observations, Proctor (1961) experimented with the possibility that this liverwort was dispersed by ducks. He used three Mallard ducks (*Anas platyrhynchos*; Figure 77) that had been used previously for similar experiments with the alga *Chara*. These ducks were provided with approximately 57 liters of the *Riella americana*, which they readily ate. The plants had abundant sporophytes with what appeared to be mature brown spores. The feces were collected after approximately 1 hour and handled according to treatments in Table 3. The feces contained many spores that had separated from their masses, no intact sporophytes, and thallus fragments that were clearly dead. Feces were collected for three days, and on the third day they were separated by individual duck. It was interesting that one male and one female had numerous spores in their feces, but the second female had none! Germination success ranged from 0 - >30%.

Table 3. Various storage effects on germination of *Riella americana* spores collected from Mallard duck feces. Germination follows 60 days of treatment, then 14 days of inoculation at 24°C on sterile tubes of soil and water in light. + = <10% germination; ++ = 10-30% germination; +++ = >30% germination; - = no germination; blank = not enough spores for test. Based on Proctor 1961.

	day 1	day 2	day 3 male	day 3 female
ice (-10°C)	++	+		
water at 1°C	+++	+++	+++	+++
water at 24°C	+++	+++	+	+
water at 37°C	+++	+++	+++	+++
dried, stored at -10°C	-	+	++	++
dried, stored at 24°C	+++	+++		
dried, stored at 37°C	+++	+++		

Proctor (1961) found that the spores of *Riella americana* (Figure 78) from feces germinated as well as fresh spores (not eaten). These spores mature at the time ducks and other water birds are migrating through that area of Texas in early autumn, so their transport through water bird guts is quite possible. Proctor (1961) suggests that many spores can be transported in the gut for up to 80 km. Furthermore, as already suggested by Studhalter (1932) and Persson and Imam (1960), external transport of spores and even fragments on feathers, beaks, and feet is a likely possibility. This notion is supported by the presence of spines on the spores (Figure 78) (Studhalter 1933). Furthermore, the spores have sufficient longevity to survive in muds or on birds (3 years for *R. americana*, 12 years for *R. capensis*). And it is possible that some remain in tetrads during dispersal, further protecting them from UV light and desiccation. Considering these dispersal potentials, it seems that something else must explain the rarity. Perhaps there is too much herbivory before they can become established? Could timing be important to avoid herbivory during establishment?

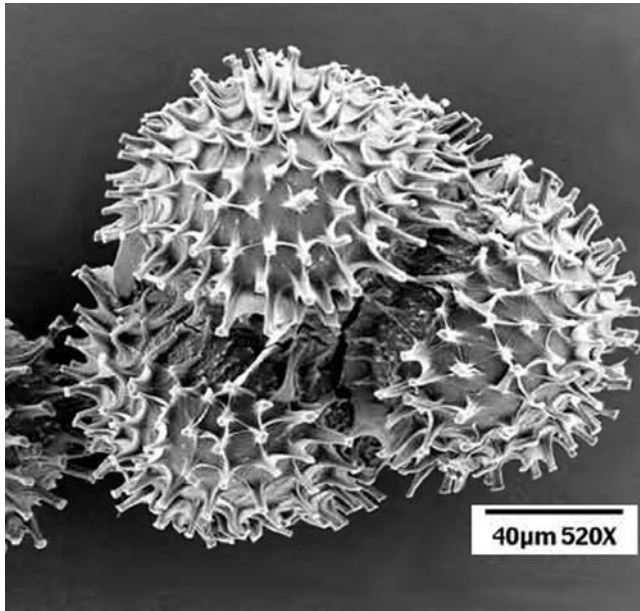


Figure 78. *Riella americana* spore tetrad SEM, exhibiting spines that could attach to feathers of ducks. Photo by William T. Doyle, with permission.

Riella is not the only bryophyte to experience dispersal by ducks. Des Callaghan (Bryonet 26 August 2016) reported that his friend had sent him a moss shoot grown from a fragment in a Mallard dropping (*Anas platyrhynchos* (Figure 77). This turned out to be the moss *Didymodon insulanus* (Figure 79).

Recent studies have revealed that other birds may also be dispersers. Using fecal samples from the herbivorous Upland Goose (*Chloephaga picta*; Figure 64) and White-bellied Seedsnipe (*Attagis malouinus*; Figure 80), Behling *et al.* found vegetative diaspores, including various moss fragments. Experiments continue to determine their viability. *Attagis malouinus* feeds among the low vegetation, sits among the mosses, and may even spread its wings across the mosses in the tundra, affording numerous opportunities for snagging the local bryophytes.



Figure 79. *Didymodon insulanus*, a species whose fragments survived the digestive tract of a Mallard. Photo by David T. Holyoak, with permission.



Figure 80. *Attagis malouinus*, a species that carries bryophyte propagules among its feathers. Photo by Jacob Wijpkema <jacob.wijkema@gmail.com> & Tini Dijk <tini.wijkema@gmail.com>, with permission.

Just imagine how far diaspores might travel by **ecto-zoochory** (on the outside of an animal) among the bird plumage. We know birds survive airplane travel, so bird travel is not a stretch. And the idea is not so far-fetched when we consider the number of bipolar species of bryophytes and the number of birds that travel those same distances from Arctic to the Antarctic. Lewis *et al.* (2014) developed a method to screen feathers of wild birds that travelled these long distances in their annual migrations. They concluded that the entire flock of migrating birds may leave their northern breeding grounds carrying potentially viable propagules, providing opportunities for dispersal everywhere they land to feed or rest.

Szepesfalvy (1955 in Schuster 1966) found *Riccia frostii* (Figure 81) concentrated along goose paths in central Hungary and suggested that the spores of this species were distributed on feet and beaks of these domestic geese. And we cannot, without testing it, eliminate the possibility of distribution of spores in feces (Figure 82), although it would require having the geese eat something that ate the spores or carried them on its surface. Szepesfalvy also suggested that spores and overwintering thallus pieces of *Riccia bischoffii* var. *ciliifera* (Figure 83)

are distributed by pheasants, but both of these suggestions are based on circumstantial evidence and the correlation may be one of habitat rather than dispersal agent. Furthermore, these birds are surely not the only animals to frequent these paths. Szepesfalvy also suggested a relationship between presence of hares and distribution of *Oxymitra paleacea* (Figure 84), but this meets the same problem of verification.



Figure 81. *Riccia frostii*, a liverwort that can concentrate along goose paths, presumably due to having the geese spread the spores. Photo by Rosemary Taylor, with permission.



Figure 82. Canada Goose (*Branta canadensis*) dung at a wildlife station, Ohio, USA – a potential dispersal mechanism. Photo by Janice Glime.



Figure 83. *Riccia bischoffii* var. *ciliifera*, a species with overwintering fragments that may be dispersed by geese. Photo by Jan-Peter Frahm, with permission.



Figure 84. *Oxymitra paleacea*. Photo by EncycloPetey, through Creative Commons.

Brandon Stone reported to Bryonet (9 April 2003) that he found sporophytes of the moss *Pyrrhobryum spiniforme* (Figure 85) in a bird's nest at 1300 m on Moloka'i in Hawai'i. A bird expert told him the bird was most likely not a native bird. Transport of such sporophytes at the right stage could contribute to dispersal over more than the normal range of dispersal from capsules on the ground.



Figure 85. *Pyrrhobryum spiniforme* showing sporophyte that is used in making birds' nests in Hawaii. Photo by Michael Lüth, with permission.

Several birds frequent upturned roots where *Schistostega pennata* (Figure 86) is common in Russia, and there is evidence that these may transmit spores (Ignatov & Ignatova 2001). The tiny Winter Wren (*Troglodytes troglodytes*; Figure 87-Figure 88) visits upturned roots to look for insects and sometimes nests there. Above one nest near a convenient perch, there were protonemata of *S. pennata*, suggesting they may have arrived as spores on the birds.

A more convincing case of bird dispersal is that of the cock *Tetrastes bonasia* (Hazel Grouse; Figure 89) (Ignatov & Ignatova 2001). These large birds take dust baths near the upturned roots. Feathers collected there did have spores of *S. pennata* attached. However, no chloroplasts seemed to be present, so it is unlikely that they were still viable. The birds also help in dispersal of spores by capturing beetles such as *Geotrupes* (Figure 90) with adhering spores and distributing their parts to other locations. Mice and frogs also visited tip-up areas, but there was no direct evidence that they transported spores.



Figure 86. Capsule and seta of *Schistostega pennata*. Note the delicate, white stalk and the sticky spores on the outside of the capsule. Photo with written permission from Misha Ignatov.



Figure 87. *Troglodytes troglodytes* (Winter Wren), known to build nests near good locations for *Schistostega pennata*, possibly transporting spores. Photo by Sonja Kübelbeck, through Wikimedia Commons.



Figure 88. *Troglodytes troglodytes indigenus* on a moss-covered tree from Kuwait, a winter wren that might disperse bryophyte spores to a perch above its nest. Photo by Bob McCaffrey, through Creative Commons.



Figure 89. *Tetrastes bonasia* (Hazel Grouse) transports bryophyte spores and also eats beetles that carry them, but viability of the spores is unknown. Photo by Kallerna, through Wikimedia Commons.



Figure 90. *Geotrupes stercorarius* on moss, a beetle species that can carry spores, then get transported farther when captured by birds. Photo by Thomas Bresson, through Wikimedia Creative Commons.

We have already noted that slugs can carry viable spores in their digestive tracts. Birds eat slugs. Could it be that the spores could survive both digestive tracts? Wada *et al.* (2011) addressed this very question. Japanese land snails are preyed upon by birds, including the Japanese White-eye (*Zosterops japonicus*; Figure 91) and the Brown-eared Bulbul (*Hypsipetes amaurotis*; Figure 92). Of the 119 snails (*Tornatellides boeningi*; Figure 93) fed to Japanese White-eyes and 55 snails fed to Brown-eared Bulbuls, 14.3% and 16.4% of the snails, respectively, passed through the gut alive. For us, the logical next question is whether this provides an additional means of dispersal for bryophyte spores, potentially giving them a free ride to greater distances while being protected from the

bird's digestive system by the snail. Kawakami *et al.* (1965) suggested that it is.



Figure 91. Japanese White-eye (*Zosterops japonicus*). Photo by Ltshears, through Creative Commons.



Figure 92. Brown-eared Bulbul (*Hypsipetes amaurotis*). Photo by Lip Kee Yap, through Wikimedia Commons.



Figure 93. *Tornatellides boeningi*, a species that can pass through bird guts and survive. Photo by Shinichiro Wada, through Creative Commons.

Griffin *et al.* (1982) suggested that *Dendrocryphaea latifolia* may have reached the high Andes of Colombia by wind or birds, but there is no direct evidence to support this.

As Ken Adams suggested on Bryonet (5 March 2013), birds might occasionally be responsible for long-range bryophyte dispersal. Spores could lodge on or among feathers or feet, especially in mud, protecting them from both desiccation and UV light. Michael Richardson (Bryonet 5 March 2013) suggested that this could occur as short hops (stepping stones), with birds depositing spores at resting or feeding points along the way. When those establish, they provide a new and closer source for dispersal to more distant locations. Richardson suggested that gulls might be good vectors because of their need for fresh-water baths and their puddle-hopping behavior. Terry McIntosh (Bryonet 5 March 2013) suggested that birds may account for some of the wide disjunctions in western North America for species that are restricted to open soil in the grassy edges of saline ponds and depressions. This could explain the distribution of such species as *Entosthodon rubiginosus* and *Tortula nevadensis*.

Fife and de Lange (2009) suggested that shearwaters (*Procellariidae*; Figure 96) may have been responsible for transporting propagules of the pan-tropical *Calymperes tenerum* (Figure 94) to the Chatham Islands and Kermadecs off the coast of New Zealand. These fantastic birds fly from Alaska to Australia and other parts in the deep Southern Hemisphere, then back to Alaska each year.



Figure 94. *Calymperes tenerum* with gemmae. Photo by Jan-Peter Frahm, with permission.

Jesús Muñoz (Bryonet 15 March 2013) studied the effects of wind on Cory's Shearwater (*Calonectris diomedea*; Figure 95) migration and suggested that it might be worth investigating those same wind patterns for bryophyte dispersal. Earlier in this chapter I suggested that propagules might follow "wind highways." Could this following be in the protection of the feathers and mud of birds? Felicísimo *et al.* (2008) used a model to show that the Cory's Shearwaters closely follow the "wind highways" that require the least energy to reach their breeding and wintering areas. The Manx Shearwaters (*Puffinus puffinus*; Figure 96) chose a route that was 25% longer, avoiding turbulence on the shortest distance (González-Solís *et al.* 2009). The wind patterns (not the shortest route) drive the shearwaters in their movements and could do the same for bryophytes (Felicísimo *et al.* 2008; González-Solís *et al.* 2009).



Figure 95. *Calonectris diomedea* (Cory's Shearwaters). Photo by Antlewis, through Creative Commons.



Figure 96. Manx Shearwater (*Puffinus puffinus*) in Iceland, a potential bryophyte dispersal agent. Photo by Chiswick Chap, through Creative Commons.

Brent Mishler (Bryonet 5 March 2013) suggested that vegetative fragments could travel in mud on birds' feet as well, and that molecular testing could be used to track such long-distance dispersal. Rob Gradstein (Bryonet 11 March 2013) suggests a less molecular, more challenging approach: 1) capturing migratory birds to look for bryophyte spores, gemmae, and fragments on their feathers, feet, and beaks; 2) flying spores, gemmae, and fragments on birds across long distances to test for germinability of the diaspores after the long trip.

Even feet of terrestrial birds can carry spores, and probably other propagules. Davison (1976) reported finding spores of bryophytes on the feet of the Song Thrush (*Turdus philomelos*; Figure 97) in beechwood in Great Britain, although he considered that these were transported only a short distance.

Even the tiny hummingbird may contribute to long-distance dispersal of bryophytes. Torres-Dowdall *et al.* (2007) reported the use of bryophytes in the construction of nests of the hummingbird called Picaflor Rubi (*Sephanoides sephanioides*; Figure 98-Figure 99) in Chile. Osorio-Zuñiga (2012) later examined the nests of the Picaflor Rubi (also known as Picaflor Chico). He identified *Lophosoria quadripinnata* (a tree fern), appearing as the "garment" in 100% of the nests, and three moss species, all pendent species, that frequently comprised the outside of the nests [*Weymouthia*

cochlearifolia (16.6% of nests) (Figure 100), *W. mollis* (26.6%) (Figure 101), and *Ancistrodes genuflexa* (100%) (Figure 102-Figure 103). These outside mosses all produced sporophytes in both the old and new nests (Figure 106-Figure 108). In addition to these species, old nests also had *Eriodon conostomus* (Figure 104), *Ptychomnion ptychocarpon*, and *Dicranoloma robustum* (Figure 105), all producing sporophytes (Figure 108). For species present in 100% of the nests, the growing heights were 10-18 m above ground and were not the most abundant species in the forest.



Figure 97. Song Thrush (*Turdus philomelos*), a bird known to carry moss spores on its feet. Photo by Taco Meeuwssen, through Wikimedia Commons.

In continuing this study, Osorio-Zuñiga *et al.* (2014) introduced the concept of **synzoochory** for bryophyte dispersal as an intermediate between endo- and ectozoochory. In **synzoochory**, the propagules are deliberately transported, usually by mouth or beak, but without ingestion. These researchers found seven species of mosses were transported this way by the hummingbird *Sephanoides sephanioides* (Figure 98). These likewise were to be used in nests, but the researchers found that the birds were selective, choosing mosses with capsules in greater frequency than their appearance in the habitat. They also preferred the fern *Lophosoria quadripinnata* and the moss *Ancistrodes genuflexa* (Figure 102-Figure 103), with the other mosses [*Weymouthia mollis* (Figure 101), *Weymouthia cochlearifolia* (Figure 100), *Eriodon conostomus* (Figure 104), *Ptychomnion ptychocarpon*, *Dicranoloma robustum* (Figure 105), *Rigodium toxarion*] being minor components. This behavior of the birds gave two opportunities for greater dispersal – first from one tree to another in the beak, then for longer distances for the spores from the elevated position of the nest. In some cases the mosses were elevated from the ground to the nest.



Figure 98. Picaflor Rubi (*Sephanioides sephanioides*), a hummingbird that selects mosses for her nest. Photo by Suemili, through Wikimedia Commons.



Figure 100. *Weymouthia cochlearifolia*, a pendent moss used in the nests of the Picaflor Rubi. Photo by Juan Larrain, with permission.



Figure 99. *Sephanioides sephanioides* on moss-constructed nest, looking quite camouflaged. Photo by Diucón, through GNU Free Documentation.



Figure 101. *Weymouthia mollis*, a pendent moss that is placed on the outside of the nests of the Picaflor Rubi. Photo by Juan Larrain, with permission.



Figure 102. *Ancistrodes genuflexa*, a pendent moss used in the outside of the nests of the Picaflor Rubi. Photo by Felipe Osorio Zúñiga, with permission.



Figure 103. *Ancistrodes genuflexa* with capsules. Photo by Felipe Osorio Zúñiga, with permission.



Figure 104. *Eriodon conostomus* with capsules. Photo by Juan Larrain, through Creative Commons.



Figure 105. *Dicranoloma robustum*. Photo by Juan Larrain, through Creative Commons.

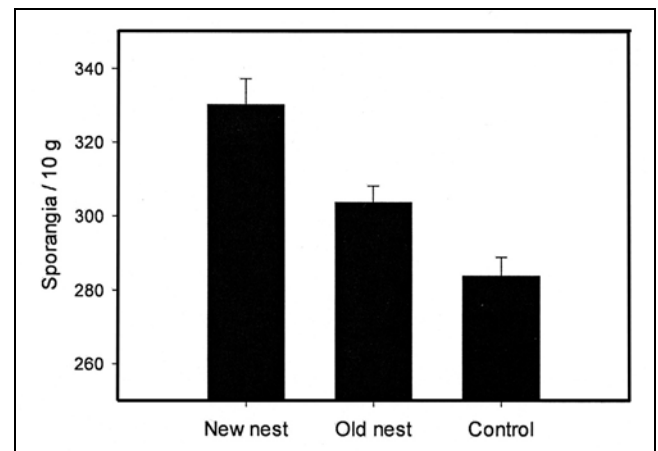


Figure 106. Sporophyte number vs nest age in 10 g of nest mosses for the Picaflor Rubi (*Sephanoides sephanioides*). Redrawn from Osorio Zúñiga (2012).

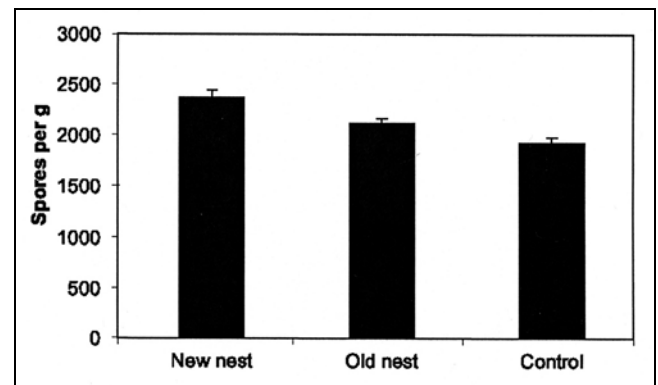


Figure 107. Effect of nest age on spore number per gram of moss in nests of the Picaflor Rubi (*Sephanoides sephanioides*). Redrawn from Osorio Zúñiga (2012).

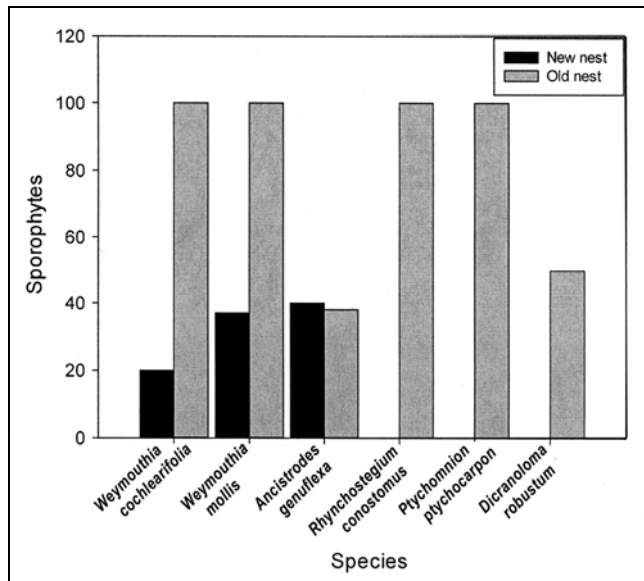


Figure 108. Number of sporophytes compared to nest age for bryophytes in nests of the Picaflor Rubi (*Sephanoides sephanoides*). Redrawn from Osorio Zúñiga 2012.

As noted above, members of the **Splachnaceae** are known for their ability to attract flies that subsequently disperse their spores. But it appears that this is not always the case. Lewis *et al.* (2014) considered the long-distance dispersal that was evidenced in *Tetraplodon* (Figure 55, Figure 58-Figure 59). The amphitropical disjunctions required explanation. The researchers compared stepwise migration along the Andes, direct long-distance dispersal, and ancient vicariance. Using four loci from each of 124 populations throughout the global range, they analyzed genetic evidence for the dispersal pathway. Three clades emerged, indicating three pathways of dispersal. There is no evidence of modern or historical wind connectivity between the polar regions, and these spores are not easily dispersed by wind. The researchers concluded that migratory birds most likely accounted for the long-distance dispersal of *Tetraplodon*, suggesting that the order Charadriiformes were the most likely dispersers.

Additional information on birds that eat capsules is in Volume 2, Chapter 16-2.

Mammals

Both large and small mammals step on bryophytes. Fur and hooves are likely to carry at least some forms of bryophyte propagules. Pauliuk *et al.* (2011) investigated dry grassland dispersal by sheep. They collected gametophyte fragments from the fleeces and hooves of 12 sheep, including two breeds. They also grew microscopic diaspores collected from soil that adhered to the hooves. Among the species in the pasture, 40% were transported, comprising 16 moss species. Sheep breeds collected different arrays of species, with dense, curly fleece carrying more fragments and larger species than sheep with smooth and fine hair. Pleurocarpous species, small species, and mats were represented more frequently in proportion relative to the vegetation; large species, acrocarpous life forms, wefts, and turfs were underrepresented. Hooves carried mostly acrocarpous colonist species.

In the Arctic, *Voitia hyperborea* (sometimes considered a variety of *V. nivalis*; Figure 25) has a capsule that does not open (Steere 1974). It appears that musk oxen and caribou may help in dispersal by chewing on the capsules as they graze other plants. In any event, it would seem that some animal agent is necessary for the dissemination of spores. During (personal communication, 29 May 2006) suggested that whole capsules may possibly be dispersed, but that the spores in *Voitia nivalis*, at least, have a structure that suggests they are sticky like those of other genera of the **Splachnaceae** and may adhere to beetles or even larger animals once the capsule begins to decay and expose them. More detail on the dung mosses is in the habitat subchapter on dung mosses.

In the Alps, *Voitia nivalis* is apparently dispersed by ruminants. It can be found in shelters or on the trails of sheep, chamois, and ibex, often on dry cliff ledges (Geissler 1982). This dispersal could carry fragments and other diaspores trapped on the feet and among fur or through feces holding spores inadvertently eaten along with forage.

There is some evidence that rodents contribute to the dispersal of fungal spores through ingestion and subsequent deposit of feces (Trappe & Maser 1976; Cázares & Trappe 1994; Janos *et al.* 1995). It is likely that rodents likewise contribute to bryophyte spore dispersal, not only through ingestion, but also by transporting spores in their fur. Others are likely to hitch a ride in mud on the feet. Nevertheless, it appears that direct data to support this role are lacking for bryophytes. We do know that rodents eat bryophytes, as shown for this mouse dining on *Funaria hygrometrica* capsules (Figure 109). Andrew Spink photographed a vole eating mosses (Figure 110).



Figure 109. Mouse eating *Funaria hygrometrica* capsules on Isle Royale, Michigan, USA. Photo courtesy of Steve Juntikka.

Matt Dami (Bryonet 26 August 2016) reported providing mice with capsules of the mosses *Dicranum flagellare* (Figure 111) and *Polytrichum commune*. They consumed the capsules and the fecal samples were collected and cultured on nutrient agar. Both species grew from the ingested spores, but *P. commune* (Figure 112) had much more germination success and far more vigorous growth.



Figure 110. Bank vole eating mosses in The Netherlands. Such close contact is likely to carry spores from the capsules seen in the picture. Photo by Andrew Spink, with permission.



Figure 111. *Dicranum flagellare*, a species whose spores survive the digestive tract of a moss. Photo by Bob Klips, with permission.



Figure 112. *Polytrichum commune* with capsules. Their spores seem to thrive when passed through the digestive tract of a mouse. Photo by Bob Klips, with permission.

Spores adapted for animal dispersal are sticky and elliptical, as in *Splachnaceae* (dung mosses) or *Schistostega pennata* (luminous moss), these being dispersed by flies. Beetles, earthworms, and slugs are likely dispersers, albeit for short distances. Ducks are known to carry spores, and small nesting birds may use setae and capsules in nests, but the effectiveness of these dispersal agents is unknown.

Water Dispersal

Conrad (1996) examined water samples in a *Taxodium* (bald cypress) swamp biweekly for spores. He also cultured both herbarium specimens and propagules from the diaspore bank. Although two other liverwort species regenerated from soil diaspores, *Ricciocarpos natans* (Figure 113) grew only from the spores (Figure 114) in the water samples and Conrad concluded that its presence in the swamps is entirely due to water dispersal.



Figure 113. Floating thalli of *Ricciocarpos natans*. Photo by Janice Glime.

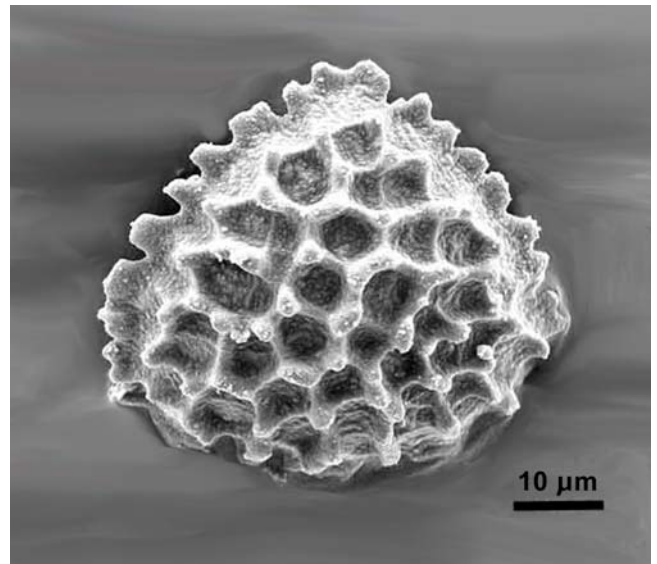


Figure 114. SEM of *Ricciocarpos natans* spore, a spore most likely transported by water. Depressions in the surface may aid in flotation. Photo by William T. Doyle, with permission.

Aquatic liverworts often have spines on their spores. Porsild (1903) believed that these served as attachment aids for spore dispersal by aquatic animals. However, other scientists believe that they instead act as anchors to hold

the spores onto rough surfaces so that not all are lost during heavy flows of streams (Studhalter 1933). In any case, some aquatic species, e.g. *Ricciocarpos natans* (Figure 114) and *Riccia fluitans* (Figure 115), do not have these spines, suggesting that the surface configuration may have more to do with phylogeny than with environment. On the other hand, they may aid flotation, permitting the water to carry them off.

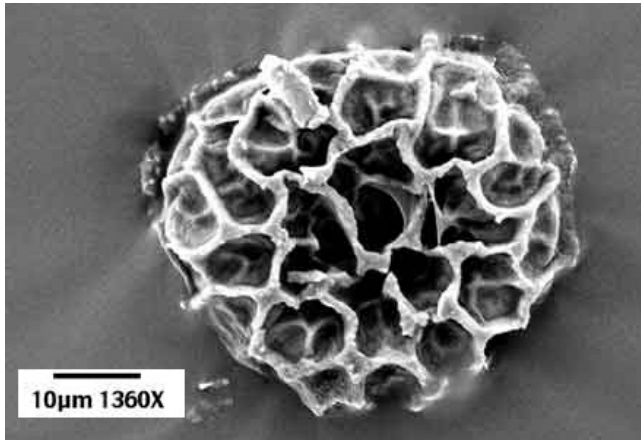


Figure 115. *Riccia fluitans* spore distal view SEM. Photo by William T. Doyle, with permission.

It is fairly common for rock-dwelling bryophytes of streams and rivers to project their sporophytes above the water level where they can be wind dispersed (Figure 116). This requires timing to produce sporophytes at a time when the water level is down.



Figure 116. *Hygrohypnum alpinum* with emergent capsules. Photo by Michael Lüth, with permission.

Common Adaptations

Mahabalé (1968) reviewed the characteristics of spores of aquatic tracheophytes. He found that the spores are short-lived and germinate quickly. These are water-dispersed. Those that are semi-aquatic or are facultatively aquatic have spores with thick outer walls and are dispersed by either insects or wind.

Cox (1983) tested the hypothesis that aquatic spores would have large, long axes and move in planes such as the

water surface, rather than in three dimensions. He also predicted a greater incidence of dioicism. He found that data supported these hypotheses for a variety of aquatic spores, including bryophytes. He also found that many spores had flotation devices. Cox considered these traits to provide "an efficient search vehicle." He considered dispersal in the aquatic environment to be a random search and that movement in one plane reduced that search territory.

As Mahabalé suggested, spores of the liverwort *Riccia gougetiana* (Figure 117) are over 200 μm in diameter (Schuster 1966); those of *Riella* (Figure 78) are 70 μm , nearly four times as large as the diameters of most air-dispersed spores (Mahabalé 1968; Cox 1983). *Pellia epiphylla* (Figure 118-Figure 119), a common streamside species, disperses its spores as a single mass (Cox 1983), but it also has elongate spores (Figure 119). *Gymnocolea* (Figure 120) uses deciduous perianths as its floating dispersal unit. Elongate dispersal units are seen in vegetative dispersal units such as fragments of *Fontinalis* (Figure 121) (Glime *et al.* 1979).



Figure 117. *Riccia gougetiana*, a species with 200 μm spores. Photo by Jonathan Sleath, BBS website, with permission.



Figure 118. *Pellia epiphylla* capsule dehiscent, showing clumps of spores. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 119. *Pellia epiphylla* spore. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

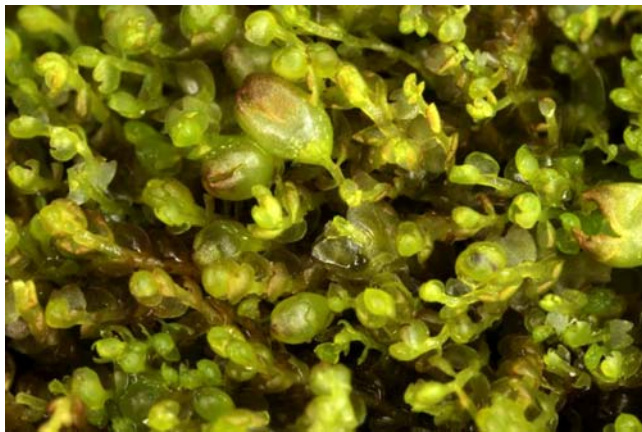


Figure 120. *Gymnocolea inflata* showing enlarged, oblong terminal perianths. Photo by Jan-Peter Frahm, with permission.



Figure 121. *Fontinalis dalecarlica* fragments imbedded in ice from a stream in New Hampshire, USA. Photo by Janice Glime.

Marine Dispersal?

No species is known to grow in marine waters, but Engel and Schuster (1973) raised the question of marine dispersal. They reasoned that species subject to tidal action or ocean spray were the best candidates. They assumed that bryophytes would not survive long exposures to salt water and presumed that freshwater drainage from adjacent forests above the beach and high rainfall made it possible

for species subjected to saltwater to survive. Hence, they concluded that marine dispersal was not possible, but this has not been tested.

Flood Plains and Dry Flats

Volk (1984) suggested that the distribution of spores by animals is most important for genera like *Riccia* (Figure 117) that inhabit seasonally dry habitats, particularly in southwest Africa and the Mediterranean. Whereas annual species of *Marchantiales* produce large numbers of spores, in the perennial species spore number is typically reduced and is even more rare among species with bulbils. Those that do support significant spore production can have ornamented spores that facilitate transport by animals, or perhaps aid in flotation. Despite the periodic invasion by water, this may not be an effective means of dispersal to carry the spores to new locations. Large flooding episodes can bury spores and other propagules so much that they may not resurface for decades (Figure 122-Figure 123).



Figure 122. Eroded material transported by water to River Baihe, a tributary of Yellow River, Tibet. Photo by Sven Bjork, with permission.



Figure 123. Floodplain on Isle of Wight. This magnitude of flood is reached once in ten years. Photo through Wikipedia Creative Commons.

Schuster (1966) considered the dispersal of *Riccia* (Figure 124) and *Ricciocarpos* (Figure 114) spores by mud and water to be very frequent. They typically grow at the margins of rivers and streams in the floodplain, where their spores mature in spring or in late summer or fall when flooding is common. The hornwort genus *Notothylas* (Figure 125) is also likely to be dispersed in this way. In *Riccia* (Figure 124) and *Sphaerocarpos* (Figure 126), the

spores are exceptionally large (65-200 μm diameter), are accompanied by elaters, and are dispersed by water.

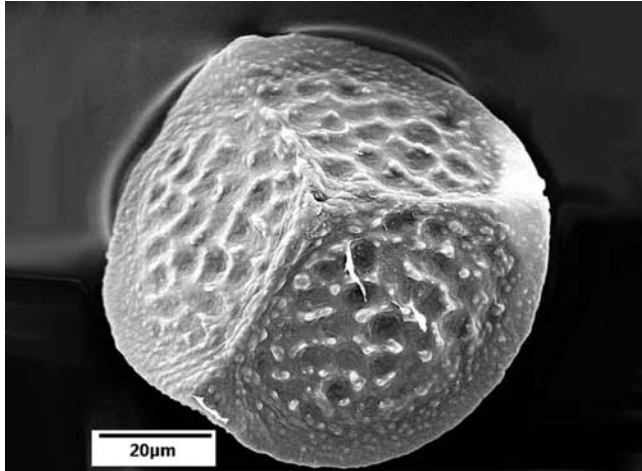


Figure 124. *Riccia beyrichiana* spore proximal view SEM, showing its larger size compared to that of *Notothylas*. Photo by William T. Doyle, with permission.

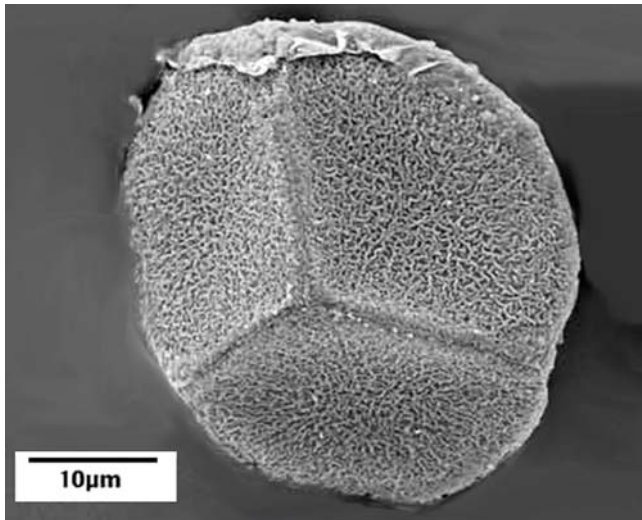


Figure 125. *Notothylas obicularis* spore proximal view SEM. Photo by William T. Doyle, with permission.

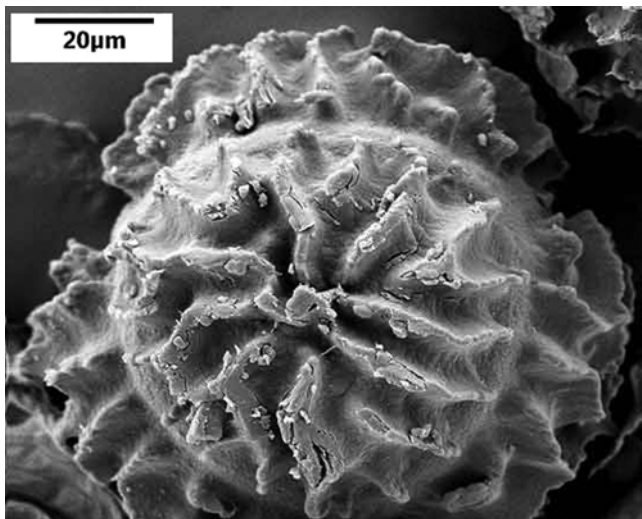


Figure 126. *Sphaerocarpos stipitatus* distal spore wall SEM. Photo by William T. Doyle, with permission.

Raindrops

The genus *Diphyscium* (Figure 127) has a flat side on its capsule. Crum (1983) reports that raindrops hitting this flat side can cause "little puffs" of spores that are propelled up to 5 cm from the capsule. It could be that the same phenomenon occurs in *Buxbaumia*.



Figure 127. *Diphyscium foliosum* flat-topped capsules where raindrops expel spores. Photo by Hermann Schachner, through Creative Commons.

Exploding Capsules?

Lacking peristome teeth, *Sphagnum* has an explosive capsule that behaves much like an air gun. It exerts an internal pressure of 4-6 atmospheres, a pressure equal to that of the "huge tires of heavy trucks" (Crum 1973). If you place mature capsules under a lamp with a tin cup or other "roof" to catch the spores, you can hear the capsules pop as the lids strike the cover, a phenomenon reported by one of the bryologists following a *Sphagnum* collecting trip at a *Sphagnum* conference in Great Britain. Some bryologists claim to have heard the capsules popping in the field, with the sound being generated entirely by the explosions of the capsules.

Vortex Rings

This explosion is a necessary event for the toothless *Sphagnum* to get its spores above the **laminar flow** region near the capsule and into the **turbulent flow** that can carry the spores away from their parent. But it seems that this is more than just a straight shot. Whitaker and Edwards (2010) report what seems to be the first evidence of plants using a **vortex ring** (Figure 128-Figure 129). The vortex ring is a self-sustaining flow field that can carry one fluid (in this case, a mass of spores) through another (in this case, the surrounding atmosphere) without significant drag. The result is that spores go farther.

When the spores explode from a *Sphagnum* capsule, this vortex ring, shaped like a mushroom cloud, forms and dissipates very quickly above the capsule (Figure 129). As the spores are ejected from the capsule, they are "entrained by the co-moving vortex bubble that forms at the lip of the capsule and moves upward" (Figure 130). The advantage of this vortex ring is that it moves the spores much farther than an air-gun mechanism could. This is the result of a self-sustaining flow field that moves the donut-shaped mass of spores upward.

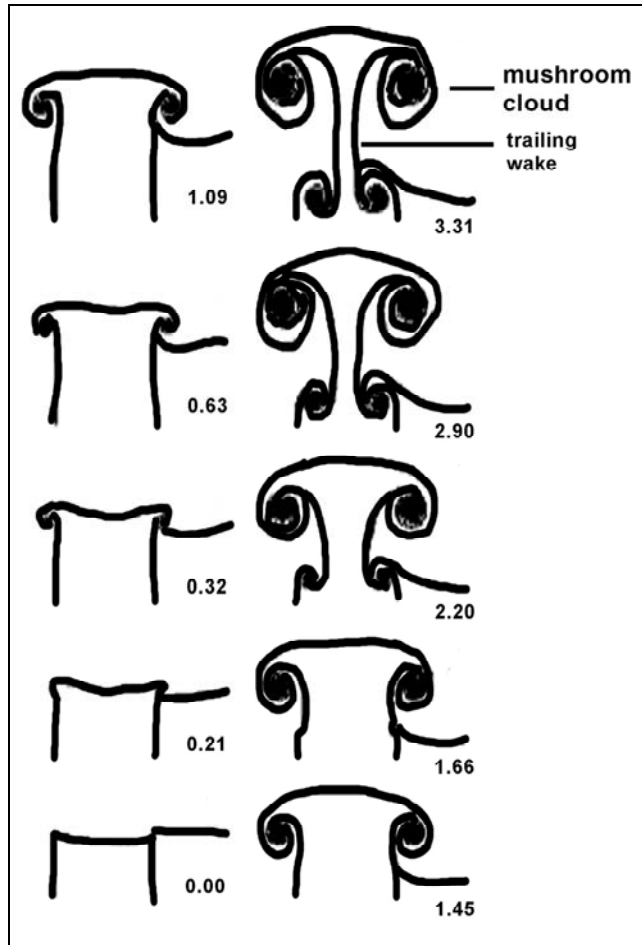


Figure 128. The development of a vortex ring with its mushroom cloud and trailing wake following the expulsion of a *Sphagnum* operculum. Redrawn from Whitaker and Edwards at <www.math.lsa.umich.edu>.



Figure 129. *Sphagnum* spore vortex taken as a time series every 100 microseconds. Photo by Clara Hard, Joan Edwards, and Dwight Whitaker from Whitaker & Edwards 2010, with permission.

The large number of spores (~100,000) in a single capsule form a bubble with a radius of 5 mm (Whitaker & Edwards 2010). These vortex rings cause a thrust augmentation by acceleration of the additional ambient fluid created at the time of the explosion (Krueger *et al.* 2008). The ring itself is "generated by the transient ejection of a jet from a tube or orifice" such as the opening of the *Sphagnum* capsule.

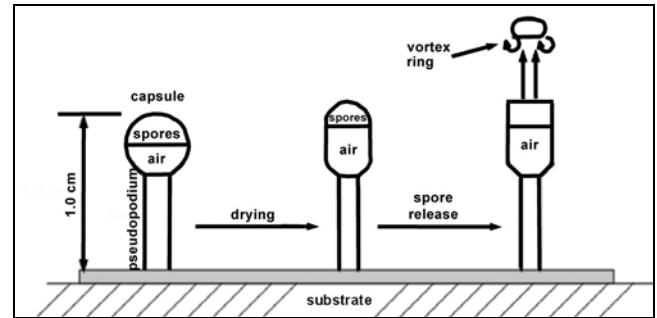


Figure 130. *Sphagnum* spore capsule from fresh to drying to release of the operculum. Redrawn from Miller 2010.

As Mustain (2010) points out, it is these vortex rings that help the squid speed through the water and the human heart to push blood from chamber to chamber. They are present in the clouds arising from an erupting volcano and propel jellyfish in the sea (Krueger *et al.* 2008). For *Sphagnum*, it permits this short plant to place its spores (Figure 131) into the winds that start about 10 cm above the surface (Whitaker & Edwards 2010). The ring keeps the spores together, preventing their useless descent to the ground. They calculated that the vortex ring typically shoots more than 11 cm into the air, sometimes as high as 17 cm. Furthermore, Johan L. van Leeuwen from the Netherlands' Wageningen University (in Mustain 2010) reports that this shot of spores reaches about 144 kph!

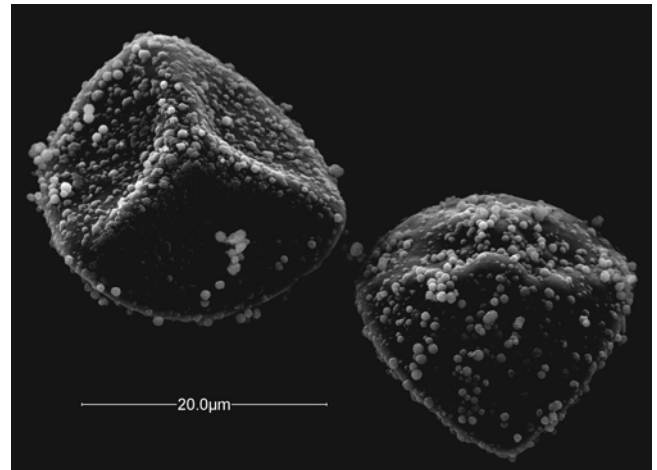


Figure 131. *Sphagnum* spores SEM. Photo by Dwight Whitaker and Joan Edwards, with permission.

Role of Stomata

Unlike many of the other bryophytes, *Sphagnum* has its stomata located away from the base and top of the capsule, suggesting that their function might be different. Boudier (1988) reported that the stomata of *Sphagnum* were not, as assumed, involved in any respiratory function in this genus, but rather that they are "false stomata" that give the capsule hardness and give the capsule wall flexibility. Beerling and Franks (2009) added to this that they were of importance in controlling and facilitating water loss from the capsule. Chater *et al.* (2011) determined that the stomata of bryophytes, like those of tracheophytes, are under the control of ABA and respond to environmental signals in the same way as guard cells of

tracheophytes. Duckett *et al.* (2009, 2010a) conducted further experiments by pricking the *Sphagnum* capsules and demonstrating that both intact and pricked capsules dried out and dehisced over an 8-12 hour period. During this time the stomatal guard cells gradually collapsed. This seems to be in direct contradiction to the assertion of Ingold (1959), who concluded that the dehiscence mechanism of *Sphagnum* capsules depends on a capsule wall that is impermeable to gases. Ingold suggested that cuticularization of the guard cells with age could block the air passage. Duckett *et al.* (2009, 2010a) contend that, rather than an air-gun explosion (as understood by Ingold), the spore discharge results when differential shrinkage of the capsule walls causes the rigid operculum to pop off.

The shrinkage of the *Sphagnum* capsule wall has been known for some time. Maier (1974) described the importance of a rigid zone of resistance in the capsule wall that permits the capsule to maintain its diameter even as the remainder of the capsule shrivels as it dries. This rigid wall tissue causes the shape of the capsule to change from spherical to cylindrical. This causes maximum stress in the area of the operculum, causing the wall (line of dehiscence) to break.

Duckett *et al.* (2009, 2010a) concluded, as did Boudier (1988), that the only role for the stomata in *Sphagnum* is to aid in capsule drying and thus shrinkage. Duckett *et al.* determined that there is no potassium-regulating mechanism for these guard cells.

The behavior of guard cells in *Anthocerotophyta* (Figure 133-Figure 136) seems to be support for the dispersal role. Lucas and Renzaglia (2002) found that the guard cells in this group do not respond to abscisic acid (ABA). Furthermore, in young tissues K^+ and malate are localized in all epidermal cells, but once the tissues mature, they occur only in the guard cells. This permits them to serve as an osmoticum that causes the guard cells to swell due to water influx. This behavior is coupled with a pattern of function in which the guard cells do not respond to light (Lucas & Renzaglia 2002; Duckett *et al.* 2010b). Rather, they begin closed in young tissues, then open as tissues mature, and remain open. This behavior permits older epidermal tissues to dry out (Figure 136). Duckett *et al.* (2010b) suggest that the same mechanism is at work in mosses. Such drying could contribute to dispersal.



Figure 132. *Anthoceros agrestis*, showing involucre where stomata are young and closed and capsule where stomata are mostly mature and open. Photo by Jan-Peter Frahm, with permission.

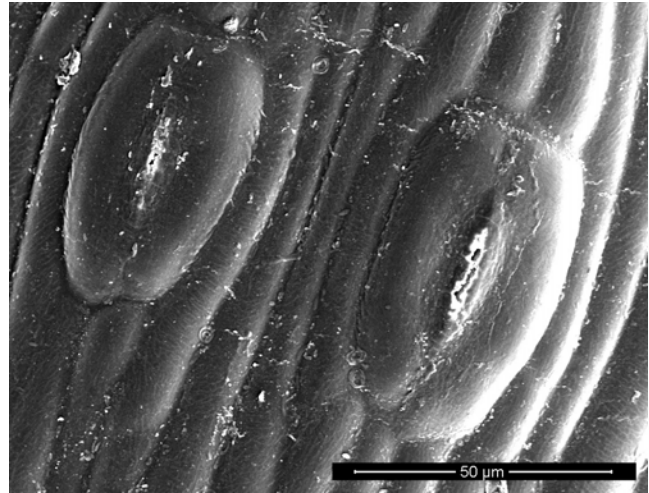


Figure 133. SEM of *Anthoceros punctatus* stomata in the sporophyte. Photo courtesy of Jeff Duckett and Silvia Pressel.

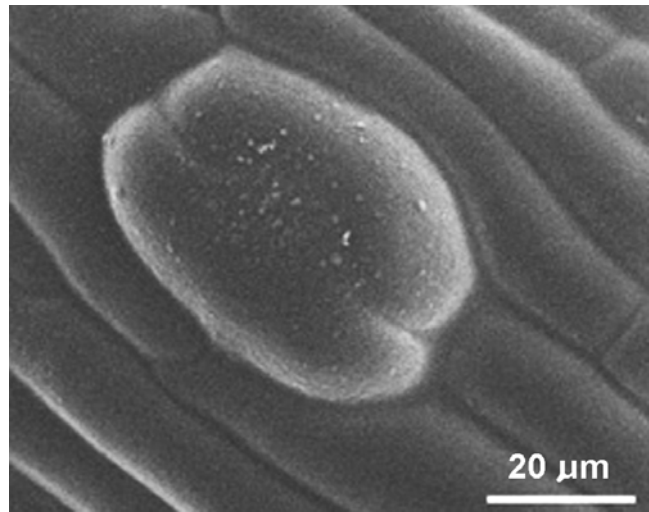


Figure 134. *Paraphymatoceros minutus* closed stoma from inside involucre. Photo modified from Jeffrey Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel, with permission.

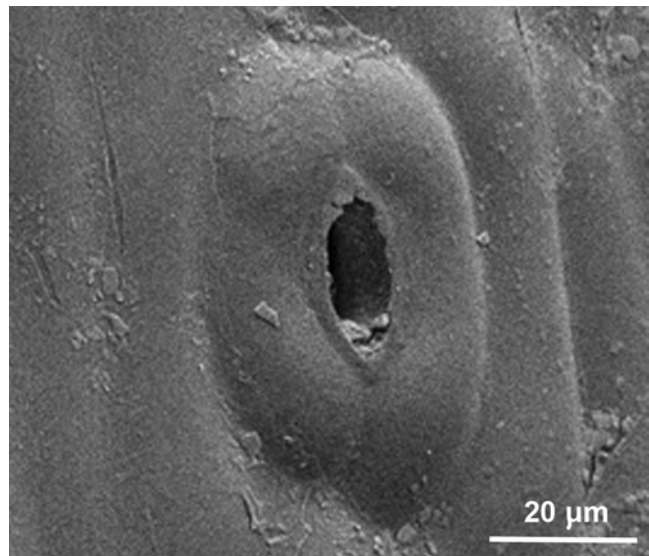


Figure 135. *Paraphymatoceros minutus* newly opened stoma from immediately above involucre, *i.e.* older tissue than that within the involucre. Photo modified from Jeffrey Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel, with permission.

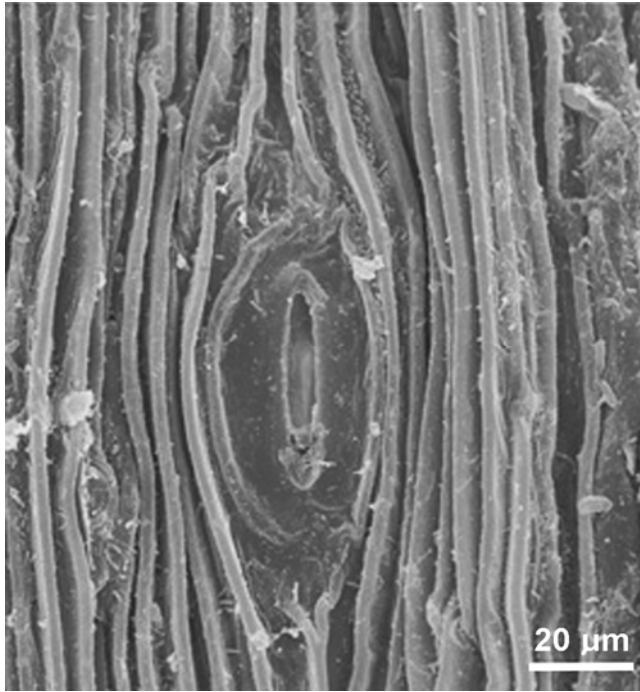


Figure 136. *Phaeoceros laevis*, open stoma flanked by desiccated and shrunken epidermal cells well above dehiscence point. Photo modified from Jeffrey Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel, with permission.

The functioning of bryophyte guard cells has been largely ignored. Pressel *et al.* (2014) followed their development in hornworts and determined that the guard cells contain giant, starch-filled chloroplasts as they begin to differentiate. These chloroplasts divide, regaining their spherical shape after the aperture opens. After opening of the guard cells, wall material accumulates over them and wax rodlets line the pores. Pressel and coworkers considered it unlikely that the guard cells moved after maturity, based on the widespread presence of open guard cells. This propensity to remain open suggests that the stomata may function in facilitating the desiccation of the sporophyte, ultimately facilitating dehiscence and dispersal.

If guard cells do indeed function to facilitate dispersal by drying the capsule, then those species with few guard cells should have diminished dispersal capacity. Sundberg (2010a) cites some species within the *Sphagnum* section *Subsecunda*, including *Sphagnum cyclophyllum* (Figure 137), *S. microphyllum*, *S. macrophyllum* (Figure 138), and *S. pylaesii* (Figure 139), as species that have small, thin-walled capsules with short pseudopodia, large opercula, and no or few pseudostomata. Hence, they have no explosive discharge of spores (Andrews 1960, 1961; Shaw *et al.* 2004). These same species have only limited geographic distribution, suggesting that the lack of stomata and explosive discharge may contribute to a limited dispersal. On the other hand, Sundberg (2010a) found that 14 boreal species with circumpolar or amphi-Atlantic distributions, including four species with a distribution also in the southern Hemisphere, (Daniels & Eddy 1990) have the explosive dispersal mechanism.



Figure 137. *Sphagnum cyclophyllum*, a species that lacks explosive discharge of spores. Photo by Blanka Shaw, with permission.



Figure 138. *Sphagnum macrophyllum*, a species that lacks explosive discharge of spores. Photo by Janice Glime.



Figure 139. *Sphagnum pylaesii*, a species that lacks explosive dispersal of spores. Photo by Michael Lüth, with permission.

But what about the role of stomata in other bryophytes? Only *Sphagnum* has the reputation of an explosive discharge. Stomatal density in non-*Sphagnum* mosses can depend on the environment, at least in some members of the *Polytrichaceae* (Figure 140-Figure 141). Szymanska (1931) found that even within the same species,

plants in moist habitats had more stomata per mm². This supports the concept that the stomata are used to help dry the capsules, although not necessarily resulting in any "explosion." Abella *et al.* (1999) found no taxonomical value for the stomata in ten species of **Pottiaceae**, so perhaps these numbers too respond to the environmental humidity or differ with habitat dryness among species within a genus.

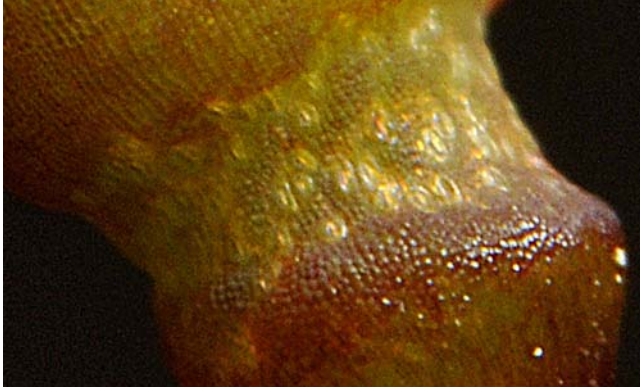


Figure 140. *Polytrichum* sp. stomata on capsule. Photo by George Shepherd, through Creative Commons.

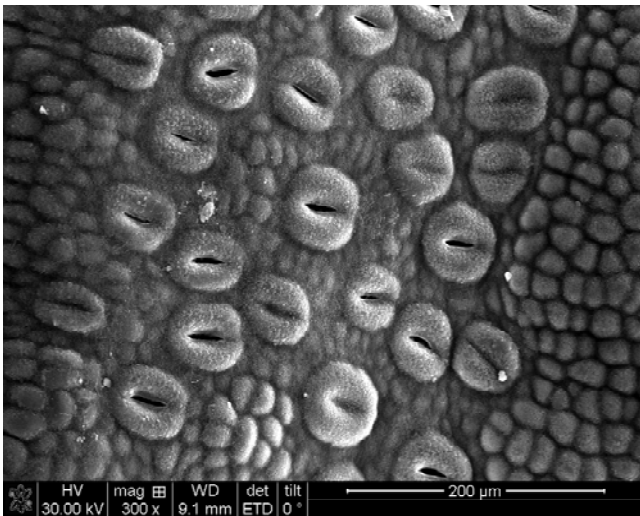


Figure 141. Stomata on neck of *Polytrichum juniperinum* capsule. Photo courtesy of Jeff Duckett and Silvia Pressel.

Egunyumi (1982) found correlations between stomata number and seta length in tropical African mosses, represented by 29 species in 12 families. These stomata ranged in number from 2 to more than 200 per capsule. This relationship might also reflect humidity of the habitat, but more data are needed to support this idea. Egunyumi found that stoma size correlated significantly with epidermal cell size, a taxonomic character. Stomatal position differed among species, with *Wijkia trichocoleoides*, *Trichosteleum microcalyx*, *Stereophyllum radiculosum* (Figure 142), and *Stereophyllum virens* having stomata raised above the level of epidermis, whereas in *Brachymenium leptophyllum* and *Bryum coronatum* (Figure 143) they were sunken.

In their work on *Funaria hygrometrica* (Figure 144), Sack and Paolillo (1983) found that subsidiary cells in that species actually have thickened walls close to the guard cell at maturity. They reported that the guard cell walls have

thin areas that are capable of flexing. The guard cell also has fibrillar layers that are oriented both axially and radially with respect to the pore. It seems that few guard cells in bryophytes have been described in such detail, but the structure is sounding a lot like that of tracheophyte guard cells. The role of stomata in spore release seems to be a promising area for research.



Figure 142. *Stereophyllum radiculosum*, a moss that has its stomata raised above the capsule epidermis. Photo by Niels Klazenga, with permission.



Figure 143. *Bryum coronatum* with capsules that have sunken stomata. Photo by Jan-Peter Frahm, with permission.

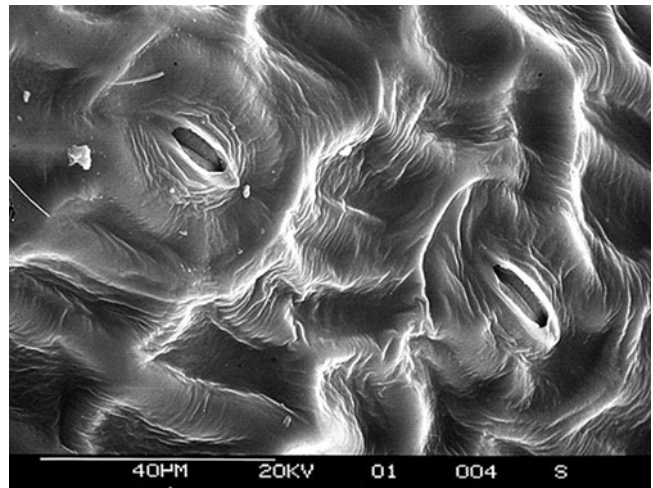


Figure 144. *Funaria hygrometrica* stomata. Photo from Botany 321 Website, UBC, with permission.

Is This an Explosion in *Sphagnum*?

Here we may have a semantic problem, with Duckett *et al.* (2009, 2010a) attempting to dispel our long-held interpretation of the method of spore expulsion by declaring it "not an air gun." But is it an explosion? While explosion can be defined as "a release of mechanical, chemical, or nuclear energy in a sudden and often violent manner with the generation of high temperature and usually with the release of gases" – certainly not descriptive of this event – the term has gained much broader meanings. Among these, we might be more comfortable with "a violent blowing apart or bursting caused by energy released from a very fast chemical reaction, a nuclear reaction, or the escape of gases under pressure." The question to be resolved is whether there are gases under pressure. Whereas Duckett *et al.* have demonstrated that the operculum is released by the distortion of the capsule, an internal pressure is necessary to qualify this as an explosion. If indeed Crum (1973) is right and the internal pressure is 4-6 atmospheres, then the release of this pressure upon dehiscence of the capsule fits at least one definition of an explosion. In any case, a vortex ring results, and that seems to be visual proof that pressure has been released.

Sundberg (2010b) disagrees with the interpretation of Duckett *et al.* (2009, 2010a) and contends that it truly is an air-gun ejection of spores. He points out that approximately 35% of the *Sphagnum* capsule volume is air. To test the role of the stomata in producing this gun, Sundberg used *S. centrale* (Figure 145) and *S. fuscum* (Figure 146). Using 16 capsules of each species, he pricked half of them in the lower half into the interior (ca 1 mm deep). Within 12 hours, all but one of the capsules had dehisced, with the ones not pricked presenting audible snaps. Spores from not-pricked capsules were ejected 50-150 mm, leaving the capsules nearly empty. The pricked capsules, on the other hand, also opened their lids, but no snap could be heard and the spores only spilled in clumps in a heap below the capsule opening, discharging only 5 mm or less. He considered this evidence that the normal discharge was explosive.



Figure 145. *Sphagnum centrale*, a species that disperses its spores explosively. Photo by Janice Glime.



Figure 146. *Sphagnum fuscum* with capsules, a species that ejects its spores explosively. Photo by Dale Vitt, with permissions.

Falling Rate

Using a filming technique similar to that of Whitaker and Edwards (2010), Sundberg (2010a) examined the settling speed of spores from 14 species of *Sphagnum*. They determined a maximum discharge speed of 3.6 m s^{-1} and a maximum height of 20 cm (mean 15 cm). The cloud (vortex ring) size was positively related to capsule size, giving species with larger capsules a dispersal advantage. Half the spores remained in clumps, usually of 2-4 spores. Single spores, with a deltoid shape, settled at $0.84\text{-}1.86 \text{ cm s}^{-1}$, a speed about 52% slower than would be expected for spherical spores of the same diameter. Larger spores settled faster, following Stokes' law. Sundberg suggested that the combination of the added height from the explosion and the slow settling speed serve to increase dispersal distance and may account for the wide distribution of boreal *Sphagnum* species. On the other hand, Fenton and Bergeron (2006) suggested that *Sphagnum* invasion into young dense forests might be dispersal limited, but they allowed for the possibility of unsuitable available substrata. It is likely also that the forest interfered with dispersal, trapping spores on bark and among the leaves.

A *Sphagnum* Spore Mimic

This spore dispersal mechanism is so good that it has been stolen by the fungus *Bryophytomyces sphagni* (Ascomycota) (Currah & Davey 2006). This parasite grows in the capsules of *Sphagnum*, replacing the *Sphagnum* spores with its own. This does nothing to interfere with the capsule explosion. Hence, the fungal spores are dispersed in that same manner as would have been for the *Sphagnum* spores.

Summary

Spores are the most successful agents of long-distance dispersal in bryophytes, whereas vegetative means help the population to become established and spread once having arrived. **Peristome teeth** in mosses, an **explosive capsule** in *Sphagnum*, and **elaters** in liverworts help in dislodging spores and dispersing them. Most bryophytes are adapted for wind dispersal, with the occasional updraft or gust permitting somewhat greater distances. However, the majority of

spores seem to land within 2 m of their parents. Invasive species seem to benefit from both rapid vegetative dispersal and long-distance travel.

Cleistogamous capsules require capsule decay for dispersal, relying on distribution by animals, especially invertebrates, or becoming established near home. Capsules of taxa like *Buxbaumia*, on the other hand, often split despite having teeth and may rely on such insects as fungal gnats to disperse spores.

Earthworms can transport spores on their moist surfaces or through the gut, and theme may be transported further if the earthworms are eaten while carrying the spores.

Animal dispersal in **Splachnaceae** and *Schistostega pennata* is facilitated by sticky, elliptical spores, and in the case of **Splachnaceae**, also by odors. Other animal dispersal appears to be chancier, with ducks, beetles, ants, slugs, earthworms, and small nesting birds contributing.

Water dispersal is important for water-dwelling species, and in floodplain taxa, a dormancy mechanism is usually necessary. Dormancy also provides spores with the ability to survive in the soil below 1 cm where they do not receive light and therefore will usually not germinate in the presence of water. Dispersal may be facilitated by decorations on the spores that create air pockets, aiding flotation. Others have spines and hooks that may aid in animal attachment and dispersal.

Raindrops on the flat side of a *Diphyscium* capsule help to discharge the spores.

Stomata seem to play a role in dispersal by facilitating drying of the capsule. In *Sphagnum*, the ejection of spores is explosive, forming a **vortex ring** that drives the spores about 10 cm into the air, enough to get them into the air stream. This mechanism is so effective that the fungus *Bryophytomyces sphagni* lives in the *Sphagnum* capsule and is dispersed by the same mechanism.

Acknowledgments

I thank Joan Edwards for her patience in helping me to understand the vortex ring mechanism. Juan Carlos Villarreal sent me literature that was not available to me. Karen Renzaglia provided images that I requested for specific purposes. Jeff Duckett and Silvia Pressel permitted me to rummage through their images to find ones I needed to illustrate this chapter. Steve Trynoski offered several suggestions after a critical reading of this subchapter.

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